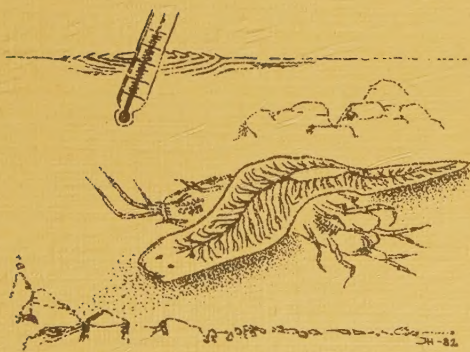


Food, reproduction and population ecology
of *Dendrocoelum lacteum* (Turbellaria)
in South Sweden

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FOOD, REPRODUCTION AND POPULATION ECOLOGY OF DENDROCOELUM LACTEUM
(TURBELLARIA) IN SOUTH SWEDEN

JAN HERRMANN

FM, Sm

DISSERTATION

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*The study of ecology is like climbing
a rounded mountain; the horizon retreats
as the climber ascends.*

T.T. Macan

ABSTRACT

Factors affecting distribution, reproduction phenology and output, population composition and feeding of the turbellarian flatworm Dendrocoelum lacteum (Tricladida) were investigated in field and laboratory experiments.

Discriminant analysis on 115 lakes showed abundance of D. lacteum to mainly depend on Asellus aquaticus, in turn due to nutrient richness via input of plant material.

The annual and semelparous D. lacteum produces cocoons in February-June, culminating in late April, hatchlings in early May. Cocoon content and sterility decreased throughout spring. Hatching time decreased with increasing temperature. Total density culminated in early July, then only juveniles. Rapid growth during autumn resulted in increasing numbers of adults throughout winter. This phenology was primarily temperature-dependent; 2°C and 10°C being approximate limits and c. 10°C optimum, supported by experiments when temporally displacing the thermal spring events. This showed the importance for triclads to adopt a proper timing of the reproductive cycle versus ambient temperature, otherwise exposing juvenile stages to vulnerable temperatures. This timing is supposed to be of adaptive value for the ultimate fitness of D. lacteum.

D. lacteum, due to its ability to take the prey and availability of these, consumed mainly A. aquaticus, less of amphipods, chironomids and oligochaetes. Raised food ration significantly increased reproductive output. Food is a major limiting factor, causing intra- and interspecific competition. Starvation caused adults to shrink more at a higher temperature, initially these also showed higher reproductive output, due to resorption of body tissue. Aggregation of triclads was attributed their feeding habits.

Compared to British D. lacteum, Swedish triclads reproduces earlier and more abundant, attributed earlier temperature rise and higher densities of A. aquaticus. Swedish triclads invest more energy on reproduction and suffer from higher intraspecific competition, leading to annual death of all adults here, whereas in Britain up to 40% live for two years; a tendency of iteroparity. Swedish D. lacteum are more of r-strategists compared to British. Reproductive timing and output is regulated by a combination of temperature and food conditions, maybe also the animals' age plays a role.



PREFACE

Throughout my years as a freshwater ecologist, I have experienced that many persons, also biologists, look somewhat sceptical when I reveal that flatworms are "my animals", and wonder what can be gained from studying these somewhat amoeboid creatures. However, this is a real underestimate of what the peculiar and less known triclads offer a researcher interested in e.g. factors regulating the reproductive biology. To their definite advantage must be said: They are easily kept in laboratory experiments; their primitive characteristics make them able cooperators; they can be easily sampled in good numbers; being predators, they take conspicuous food; they leave easily handled off-spring batches, the cocoons; finally, exposed to food shortage they show the interesting, but sometimes complicating, habit of shrinkage, or degrowth. In line with the time, I tried to focus on some ecological phenomena, with the triclad species Dendrocoelum lacteum as the object.

Curiously, there are rather few researchers in triclad ecology in the world. One of the pioneers was Anders Dahm, who inspired me to work with these, as I first regarded them, abnormal animals, and who was my supervisor during the first year. I thank him for always keeping his triclad library and knowledge accessible to me.

Very early also Per Brinck, Head of the Department of Animal Ecology, took interest in my problems and arranged, together with Anders Dahm, an important grant, allowing me to visit the famous triclad ecologist Tom B. Reynoldson, who really opened my eyes towards the triclads. Throughout the years Per Brinck has, in the background and in various ways, supported me, even if I seldom showed any signs of life from my basement room. During the last years, Per has been my supervisor, showing much understanding and patience with my different occupations, necessary to cope with everyday survival. I also thank him for his firm but kind requests for something written, and for all his questionmarks and alternative wordings in my manuscripts to improve them.

However, my supervisor for the years when most practical work was done was Staffan Ulfstrand, former the leader of the Rheoecological Group, nowadays in Uppsala. He supported with inspiring chats on experimental ideas and making manuscripts re(a)d, but also allowed me to share the Rheo-group wealthiness.

Being in this group, I could more and more gain from the practical and theoretical knowledge of all its members. Their problems and ways to solve them were often similar, although these people

mainly worked with stream animals, while I worked in a lake. For many refreshing and important discussions over my preliminary manuscripts, I especially want to thank Lars M. Nilsson, but also Björn S. Svensson and Björn Malmqvist have offered much valuable criticism. These three as well as also Christer Brönmark, Freddy Friberg, Christian Otto and Per Sjöström have formed the immediate environment, most often very friendly and tolerant to me as an intruder from the lacustrine habitat. All these persons also rapidly became my very good friends: discussing ecology in theory and practice; making field-trips for fun or "higher" purposes; having lunch or even more impressive evening meals together.

A research institute is, however, rather helpless without a competent staff of primarily non-biologists. For their assistance on the troublesome and curved research path, I really want to thank the following persons: Sune Arlebo ordered various facilities, which were, in some way, paid for by our account expert Birgitta Sundin. Ola Haraldsson and Axel Hagström never refused to, most skilfully, produce various peculiar things to the support of my practical tasks. Ulla Holmberg has always kindly allocated requested parts of her vast knowledge about books and the library, but has also patiently typed manuscripts, as also Ylva Zachrison. Astrid Ulfstrand and Steffi Douwes have professionally produced artistical figures from my less clear sketches. Last, but not least, Anne Odham typed and Gunilla Lindqvist edited the thesis in a most satisfactory way, in spite of strong time limits.

For altruistic commenting on manuscripts I am much obliged to Peter Calow, Jan Hendelberg and Tom B. Reynoldson. From the triclade horizon the world might look rather narrow, but wider ecological perspectives are, hopefully, gained from the inspiring ecology study circle, but also a good number of teaching colleagues, both animal and plant ecologists, many of these unnamed persons have also become very good friends of mine.

Financial support came mainly from funds mentioned in the papers.

As many researchers, I have often shown insignificant signs of keeping to any standard working time-tables. These my strange habits, especially pronounced this year, have meant only irregular visits at home for food and sleep. For an almost unbelievable patience with this way of life, but also continuous support and encouragement, I cannot strongly enough express my admiration and gratitude to my dear wife Inga-Lena and my beloved sons Fredrik and Jakob.

LIST OF PAPERS

This thesis is based on the following papers, which will in the subsequent summary be referred to by their Roman numerals.

- I Herrmann, J. Factors affecting the occurrence of Dendrocoelum lacteum (Turbellaria) in South Swedish lakes. - Manuscript.
- II Herrmann, J. 1979. Population dynamics of Dendrocoelum lacteum (O.F. Müller) (Turbellaria, Tricladida) in a South Swedish lake. - Arch. Hydrobiol. 85: 482-510.
- III Herrmann, J. Reproductive phenology in Dendrocoelum lacteum (Turbellaria). - Manuscript.
- IV Herrmann, J. Prey choice and its impact on the reproductive output in Dendrocoelum lacteum (Turbellaria). - Manuscript.
- V Temperature-dependence of reproduction in Dendrocoelum lacteum (Turbellaria) - an experimental approach. - Manuscript.

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SUMMARY OF RESULTS

INTRODUCTION

The freshwater turbellarian group Tricladida comprises about 120 species in Europe; the majority occurring in the southeast. In South Sweden six mainly lacustrine species are found, and these species are all chiefly predators. Life-spans differ; three of the six species complete their life-cycles in one year (Calow et al. 1981). Most ecological studies on lake tricladids have been performed in Great Britain, though little in Scandinavia.

The present study is focused on Dendrocoelum lacteum (O.F. Müller), a species easily recognized by its large size (often 15-20 mm as full-grown), wide-set eyes and lack of pigment, hence the alimentary system is often distinctly seen. From this its informative latin name is derived: Dendrocoelum = tree-like intestine, lacteum = milky-white (Ball and Reynoldson 1981).

D. lacteum occurs in a wide range of lake habitats, including moderately polluted ones, almost all over Sweden. It is also found in slowly-moderately flowing streams and brackish waters with less than c. 8 o/oo salinity. It is often found under stones, leaves and wooden debris, but also in the axils of erecting plants.

Of a variety of invertebrate prey, D. lacteum mainly takes the isopod Asellus aquaticus. Dendrocoelum lacteum hunts actively, gliding on the substrate, but an important ingredient in hunting success is its spreading of mucus, which entangles prey. When a prey is encountered, D. lacteum folds around it and sucks up the body fluid through the protrusible pharynx. Food is periodically the primary limiting resource and thus also an important factor, which through intra- and interspecific competition regulates density. Predation and infections, on the other hand, are generally regarded as of minor importance.

This dissertation, composed of five papers, describes and analyses the habitat choice, population composition, growth, reproduction phenology, feeding and temperature dependence of D. lacteum. Comparisons with British data elucidate important factors for, and strategies in the ecology of D. lacteum.

HABITAT

In a regional survey in South Sweden, 115 lakes were searched for D. lacteum (I). Lakes were characterized by collecting data on

water chemistry, vegetation and substrate, but also occurrence of other triclad species and the chief prey species A. aquaticus. Using multivariate statistical analysis it was shown that the abundance of D. lacteum was predominantly governed by the abundance of A. aquaticus. The latter was mainly correlated to the nutrient status of the lakes via presence of detritus and thereby input of allochthonous material. This relation allows D. lacteum to occur in most nutrient-poor lakes in Sweden, whereas many oligotrophic British lakes are sparsely fringed with vegetation and thus not inhabited by D. lacteum. Further, the abundance of D. lacteum seemed negatively affected by presence of mat-forming plants and positively affected by stones < 50 mm.

Lake Bysjön, 23 km east of Lund in the province of Skåne, southernmost Sweden, was chosen for field studies on different facets of the population biology of D. lacteum (II). In this lake, D. lacteum is fairly abundant, whereas two other triclad species occurred very sparsely. All D. lacteum used in laboratory experiments were also collected at this site.

Lake Bysjön is small (0.12 km^2), 8 m deep and eutrophic (conductivity $280\text{--}370 \mu\text{S}_{20} \text{ cm}^{-1}$, calcium content $55\text{--}75 \text{ mg l}^{-1}$, pH 6.8–9.7). Due to high production of phytoplankton, bottom plants and an abundant fish stock, periods of oxygen deficit occur in winter, especially in the deeper parts. The shore mainly consists of sand with varying amounts of detritus and many stones of different size. Apart from D. lacteum, the most abundant littoral invertebrates were some crustaceans, oligochaetes, gastropods, chironomids, and periodically also some other insect groups (II).

POPULATION COMPOSITION AND GROWTH

The abundance of D. lacteum on artificial stones was used to estimate the total abundance of D. lacteum. Population density culminated in early July, which was somewhat later than the peak abundance of A. aquaticus, its main food (II). The size frequency composition of the population was investigated and expressed both in terms of live length and dry weight (II). Essentially, both length and weight equally well reflected the changes in the population composition. However, weight measurements are probably more reliable, whereas length measurements are more handy and necessary if the same individuals have to be proceeded with.

Juveniles (≤ 0.25 mg or ≤ 4 mm) appeared in May-June and totally dominated the population as the reproducing adults died off (II). Although there were only moderate variations during the summer, a temporary small peak in the average size/weight of D. lacteum can be noticed (II). Initially, this was probably caused by the rapid growth of small D. lacteum, gaining weight from small A. aquaticus occurring at this time. The subsequent decrease in average weight was probably due to the size-dependent mortality of pre-adults (0.26-3.00 mg or 5-13 mm) induced by an increasing intraspecific competition for food.

D. lacteum grew rapidly during the autumn, when the prey A. aquaticus was abundant. The growth was considerably slower but continued during the winter. In January the majority of the population had reached adult size (II) with well-developed sexual organs (II).

When temperature started to rise in February, but more definite in March, the cocoon deposition began (II, III, V). After the first adults had finished their reproduction in April, they began to shrink, resulting in advancingly bad condition of the animals and eventually death (II). This gradually advancing shrinkage in combination with the appearance of hatchlings caused the population composition to change drastically throughout May, forming a complete substitution (II).

Whereas values of energy and fat content of the adults throughout the year were difficult to interpret in terms of trends, calculations of "expected weight" figures showed that the condition of D. lacteum was best in February-March and worst in July-September (II).

REPRODUCTIVE PHENOLOGY

D. lacteum is annual and semelparous (reproduces only one year). The majority of the population started the cocoon-laying in March and reached peak levels in the second half of April (II, III). The number of hatchlings per cocoon varied considerably, but a clear tendency to decrease throughout spring was evident, correlated to decreasing cocoon size (II). Based on the cocoon peak and hatching times, most hatchlings in the field were to be expected just before mid-May (III). However, in the field the apparent peak fell somewhat later, probably because the new hatchlings initially avoided the artificial stones (II). A kind of fertility measure, based on the number of adults that started the breeding season, was esti-

mated to 7.9 hatchlings produced per adult over the whole season (II).

The hatching time increased exponentially with decreasing temperature, i.e. at 5°C it lasted for about 70 days, while at 20°C 15 days were sufficient (III). These incubation times reflect the accumulated thermal energy required to hatch the cocoon. A convenient expression is the number of degree-days needed, in this case 266.

TEMPERATURE AS A REPRODUCTION PRIMER

Both field (II) and laboratory observations (V) indicated that D. lacteum did not commence reproduction, i.e. cocoon deposition, unless the temperature exceeded c. 1°C, whereas c. 20°C seemed to be an upper limit. Most cocoons were laid when temperature was in the interval 8-12°C (II,V).

It is stated (V) that selection in D. lacteum should operate towards a proper timing of the reproductive cycle in relation to and by means of the ambient temperature, ensuring that cocoons and hatchlings will occur at a thermally optimal time of the year. Otherwise these stages would be confronted with too high temperatures or increased risks of infections or predation, which would be less profitable in terms of fitness.

Also under non-rhythmic conditions, i.e. constant darkness, constant temperature (5°C) and constant food, D. lacteum showed a clear tendency to seasonal reproduction pattern, thus a kind of an intrinsic rhythmicity seemed to exist (V).

THE EFFECT OF FOOD ON THE REPRODUCTION

In laboratory choice experiments (IV), D. lacteum predominantly fed on the isopod A. aquaticus, and to a lesser extent, on the amphipod Gammarus lacustris, Oligochaeta spp. and Chironomus plumosus. Dendrocoelum lacteum seemed efficient in catching A. aquaticus, probably due to in part active search and in part that the prey frequently was entangled in the mucus spread on stones. Low catchability of G. lacustris is supposed to depend on its vigorous movements, while oligochaetes and chironomids escape hiding in the substrate.

Counted as energy percentage figures of total energy intake, these prey items formed the following proportions: A. aquaticus

55 %, G. lacustris 29 %, chironomids 9 % and oligochaetes 7 %. These figures do not differ much from what has been reported from Britain, where D. lacteum, as opposed to the present study, occurred sympatrically with other partially competing triclad species. If the present results are valid also for food conditions in the field, this would imply a case of possible but not realized ecological release, due to genetical constraints, which in this case is proposed to be attributes selected for catching especially A. aquaticus.

However, the outcome of the experiment is probably mainly a function of the general abilities to take different prey items under a certain condition and the availability of prey. Thereby, the competitive pressure from other species demanding for the same prey would still be important, but also intraspecific competition.

The reproductive output was highest when A. aquaticus was provided as food (IV). When D. lacteum was provided with increasing amounts of A. aquaticus the reproductive output rose significantly (IV).

When subjected to total starvation, D. lacteum shrank significantly, but much more so at 15°C than at 5°C (V). The output of cocoons and hatchlings decreased with time at both temperatures, but was initially much higher at 15°C than at 5°C, however, later reversing. This production of off-spring was accomplished by resorption of body tissue, thereby affecting the adults more at the higher temperature. As food has in short supply in late spring (II), it should be important for D. lacteum to terminate reproduction before temperatures become too high and metabolically unfavourable (V).

AGGREGATION

Most animals occur contagious for different reasons. The strong propensity of D. lacteum to aggregate (II) is attributed the suggestion (de Silva 1976a) that these triclad might benefit from each other by enhancing the trapping of prey in the mucus smeared underneath stones where they rest, at least at day-time (unpublished). An increased aggregative behaviour in late autumn could be due to the commencing period of copulation (II). That the aggregates are not random phenomena is indicated from density figures yielded at field experiments with concrete bricks, placed in different numerical combinations and counted at different intervals (Herrmann and Svensson unpubl.).

CONCLUDING REMARKS

Every trait of a species differs with regard to the condition it is likely to be brought up in, i.e. the average condition, which gained earlier generations and therefore can be expected to continue with reasonable predictability. Traits suitable in one locality will characterize the main part of the population there, but are less good in another locality. The adaptive value of each character is, by means of natural selection, tested by intraspecific competition and environmental constraints, also of biotic type.

As this kind of reasoning has been basic throughout my work, it has in some papers proved fruitful to compare several achieved properties and data with corresponding parameters reported for populations of D. lacteum in Great Britain. The basic idea for this is, that some factors which are critical mainly for the reproduction have turned out to differ between the investigated lake in South Sweden and the localities in middle Great Britain. The British data were mainly found in Macan and de Silva (1979), Reynoldson et al. (1965), de Silva (1976b) and Wettewé (1974), but also Calow and Woollhead (1977), and Young and Reynoldson (1966) were used. Tab. 1 summarizes the comparisons made, to some extent in a somewhat generalized way.

In Sweden the earlier temperature rise in combination with the main food A. aquaticus occurring earlier and in larger quantities allows the triclads here to reproduce earlier and with higher output, compared with British triclads. This is further enhanced by the higher numbers of hatchlings per cocoon and lower sterility percentages in Sweden. That most parameters pertaining to reproductive output are higher in Sweden is also due to the fact that the adults here are still growing during late winter, while rather shrinking in Britain.

The ratio between the recruitment factors for D. lacteum in Sweden and Britain is higher than the ratio between those for A. aquaticus (Tab. 1). This can be interpreted as if Swedish triclads invest proportionally more of their energy intake on reproduction than British do. Also, it must inevitably lead to a higher degree of intraspecific competition for food in the Swedish population (see papers II and III, and Young and Reynoldson 1966). As the latter authors indicated that young triclads can resist food shortage better than adults, these adults must be affected to a higher extent in the Swedish population resulting in a size-specific mortality. This may explain why up to c. 40 % of the adults postpone

TABLE 1

Environmental conditions for and reproductive parameter responses of D. lacteum in Swedish and British populations. Some values are based on data from more than one source.

Characteristic	Sweden	Great Britain
Temperature amplitude (monthly averages)	1 - 22.5°C	5 - 18°C
<u>A. aquaticus</u> abundance peak	early June	middle of August
<u>A. aquaticus</u> recruitment factor (maximum density/minimum density)	11.5	5 - 6
Adult weight trend at late winter	growth	degrowth
Cocoon deposition period	February-June	January-September
Cocoon deposition peak	late April	early June
Average cocoon output (numbers adult ⁻¹ month ⁻¹)	0.48	0.29
Hatching time (degree-days)	266	366
Hatchling appearance peak	middle of May	early July
Observed hatchling appearance peak	early June	middle of July
Hatchling output cocoon ⁻¹ (excluding steriles)	12 - 16	8.6 - 11.5
Cocoon sterility percentage	3 - 12	19 - 34
Fertility (young adult ⁻¹ year ⁻¹)	7.9	5.9
Total abundance peak	early July	middle of August
<u>D. lacteum</u> recruitment factor (maximum density/minimum density)	18	3 - 5
Portion of adults surviving two years	probably none	c. 1.0 %
Hatchling output response on doubled food supply to adults (increase factor)	2.33	1.13

their breeding to a second year in Britain, while in Sweden all adults seemed to die after one year of life. It is suggested (V), that the higher reproductive output of the Swedish triclads compared with British, in combination with higher energetic costs for the adults to survive another winter in Sweden, causes the Swedish D. lacteum population to be strictly semelparous. The British triclads, however, show a tendency of iteroparity, by living two years. This trade-off between reproductive output at one time and the subsequent survival chances of the parents has been called "cost of reproduction" (Calow 1979).

Most of the characteristics in Tab. 1 indicate that D. lacteum in Sweden shows traits of being more r-selected, compared with British D. lacteum, at least if one adopts a wider interpretation of this concept, i.e. more a label of environmental constraints and strategies of responding organisms (cf. Parry 1981). This is also supported by the ability of the Swedish population to respond more strongly to a doubled supply of food (V).

By a calculation of a hypothetical output in Sweden, i.e. if the triclads here had adopted the hatchling response characteristic for the British triclads, it is concluded that the delicate timing to certain temperature conditions is of adaptive value in the different regions (III). Hence, it is stated that by proper timing of the reproductive cycle in relation to and by means of the ambient temperature, D. lacteum ensures that its vulnerable juvenile stages occur at an appropriate time of the year (V). However, not only temperature, but also food availability and consumption and probably the age of the animals govern timing and outcome of the reproduction.

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FACTORS AFFECTING THE OCCURRENCE OF DENDROCOELUM LACTEUM
(TURBELLARIA) IN SOUTH SWEDISH LAKES

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ABSTRACT

By discriminant analysis on data from 115 lakes in South Sweden it was shown that the distribution and abundance of the triclad Dendrocoelum lacteum was predominantly governed by density of the isopod Asellus aquaticus, its main food. The latter was mainly correlated with the nutrient richness of the lakes, most probably via presence of proper detritus, chiefly allochthonous material. Generally, Swedish nutrient-poor lakes are surrounded by more vegetation than British ones, and are therefore mostly inhabited by A. aquaticus and consequently D. lacteum, whereas the British lakes usually lacked both species. Presence of mat-forming plants seemed to depress triclad density generally, whereas smaller stones promoted occurrence in nutrient rich lakes.

INTRODUCTION

In order to understand distributional patterns it is necessary to evaluate what factors affect the occurrence and density of the studied organism. Explanations have often involved critical thermal and chemical conditions, or dispersal constraints, less frequently biotic factors as food or competition.

Reynoldson (1966) found that productive lakes in Britain contain more species of triclads in higher abundances, than lakes with a low organic productivity. Since the pattern of distribution was not considered to be directly determined by the chemical nature of the lake water, Reynoldson suggested that the reason was the fact that the more eutrophic lakes showed a more numerous and diversified food supply. This relation is then due to the fact that among triclads, being predators, each species, to a greater extent than the other species, feeds on a particular kind of prey (see also Ball and Reynoldson 1981). There is, however, some food niche overlap, implying that also competitive exclusion could be important for the occurrence of triclads.

The annual and semelparous triclad species Dendrocoelum lacteum (O.F. Müller) inhabits both lakes and running waters in Sweden. Lacustrine populations have been shown to feed mainly on Asellus aquaticus L. (Reynoldson and Davies 1970, Herrmann 1982a). Simple cross-tabulations of the occurrence of these two species suggested that, at least when other triclad species were present, the distribution of D. lacteum largely corresponded to the occurrence of A. aquaticus (Reynoldson and Young 1966). The present investigation aims at an analysis of a material of D. lacteum in order to assess whether factors, easily studied at field work, might influence and reasonably explain the distribution and abundance of D. lacteum.

MATERIAL AND METHODS

During the summer season 115 lakes were visited; almost half of these in 1973, the remaining ones in 1979. Some additional information on substrate and vegetation was collected in 1982. As lakes in southernmost Sweden (province of Skåne) were examined in June, and the other more northern localities in July or beginning of August, phenological interference is considered marginal.

The localities, shown at Fig. 1, were chosen to represent a large range of different physiographical aspects, thus covering from very eutrophic lakes with nutrient-rich water, high production, much vegetation, and mainly soft bottom, but also pronouncedly oligotrophic lakes, oppositely characterized, and a wide range of intermediate ones. The actually sampled habitat was chosen to be representative for each lake and at the same time with moderate degree of human influence. Sampled shore-length ranged from 20 to 50 m. Effective sampling time was 30 min. For triclads suitable substrate (underside of stones, leaves, wooden debris and vegetation) was inspected and specimens found preserved in ethanol. They were later identified to species and counted.

The bottom structure at the collecting site was classified according to the dominating bottom type, i.e. detritus, clay, sand, or gravel. The prevailing type(s) was affixed value 1, the others 0. Similarly the stone size categories (< 50 mm, 50-150 mm and > 150 mm) resulted in 0 or 1 scores. Three vegetation categories were distinguished based on structural aspects: Erected plants, mat-forming plant cover and filamentous algae; occurrence of each of these was assigned 0, 1, or 2. Further, the abundance of A. aquaticus was arbitrarily given scores between 0 and 3, meaning no isopods, one or a few, sparse-fairly common, and abundant, respectively. In addition pH, conductivity, and calcium content were measured, the latter some weeks later.

Because some of the variables were of 0/1-type and far from normally distributed, discriminant analysis was chosen to trace factors influencing the distribution and abundance of D. lacteum (Nie et al. 1975). In this method, the dependent variable, here the density figures for D. lacteum, is arranged into a few categories (groups). These were defined as lakes with 0-2 D. lacteum collected per 30 min (Group 1), 3-20 (Group 2) and > 21 (Group 3). Maximum number collected in half an hour was 193 specimens. In a stepwise manner the discriminant analysis at the same time



Fig. 1. Map of South Sweden, showing all sampling localities. Filled circle denotes that *D. lacteum* was found, open circle that it was not.

compares the between-group variance with the within-group variance produced by all (remaining) variables. As a result, a list of variables is produced, where the standardized canonical discriminant function coefficients of the variables indicate the relative importance of these in discriminating between the different groups of D. lacteum densities

Green (1971) suggested that animals respond to environmental variables in a multiplicative rather than an additive manner. Therefore conductivity and calcium content were transformed to logarithms of 10, whereas all the other variables were judged too coarse for this. pH-values are already expressed on a logarithmic base. Only variables which contributed significantly ($p < 0.05$) to the discriminatory power were accepted for further computations.

RESULTS

Altogether, D. lacteum was found in 90 % of the investigated lakes, Polycelis tenuis Ijima in 70 %; Planaria torva (O.F. Müller) in 29 %; Dugesia polychroa (Schmidt) in 18 %; Dug. lugubris (Schmidt) in 10 %; and Bdellocephala punctata (Pallas) in 10 %. Thus, D. lacteum was the most wide-spread triclad in South Sweden.

The importance of the variables, treated one at a time, was seen from applying simple regression analysis. The density of D. lacteum appeared to be significantly positively correlated to four of the variables. These were conductivity, pH, calcium content ($p < 0.05$), all connected to the productivity level, and the density of A. aquaticus ($p < 0.001$).

Treating the variables simultaneously by the discriminant procedure produced a list of variables explaining most of the variation in abundance, i.e. group attachment. Group means for all variables are given in Tab. 1. These data indicate optimal values of the environmental variables for the occurrence of D. lacteum. Three variables qualified the limit of $p < 0.05$, namely A. aquaticus (positively), mat-forming plants (negatively) and Dugesia lugubris (Schmidt) (negatively) (Tab. 2). The values of the standardized canonical discriminant function coefficients show that at least the first two variables, A. aquaticus and mat-forming plants, might be the overall important ones.

The analysis produced two discriminant functions. Using the three mentioned variables, the first function contributed with

TABLE 1

A. Correlation coefficients (r) for the relations between the D. lacteum density and the different variables for all lakes.

B. Means of the variables for the three groups (different D. lacteum density) tested in the discriminant analysis. Group 1 comprises lakes with 0-2; group 2, 3-20; and group 3, >21 D. lacteum per 30 min sampling.

Variables	A		B			
	r	Signifi- cance	Means of the variables for the <u>D.lacteum</u> groups			
			Group 1	Group 2	Group 3	Total
Detritus ^a	-.078	NS	0.37	0.29	0.22	0.28
Clay ^a	.007	NS	0.11	0.22	0.15	0.17
Sand ^a	.060	NS	0.58	0.65	0.59	0.62
Gravel ^a	-.032	NS	0.47	0.42	0.59	0.49
Small stones ^{a,b}	.046	NS	0.26	0.27	0.27	0.27
Medium stones ^{a,c}	.133	NS	0.74	0.84	0.88	0.83
Large stones ^{a,d}	-.153	NS	0.26	0.22	0.20	0.22
Erected plants ^e	.111	NS	0.68	1.13	1.02	1.02
Mat-forming plants ^e	-.136	NS	0.89	0.65	0.29	0.57
Filamentous algae ^e	.146	NS	0.05	0.11	0.12	0.10
pH	.237	p<0.05	6.62	6.97	7.07	6.95
Conductivity ^f	.218	p<0.05	143	174	188	174
Calcium content ^g	.247	p<0.05	15.4	20.7	24.6	21.2
<u>Asellus aquaticus</u> ^h	.480	p<0.001	0.79	1.56	2.10	1.63
<u>Bdell. punctata</u> ⁱ	.037	NS	0.00	0.51	0.37	0.37
<u>Dugesia lugubris</u> ⁱ	-.045	NS	0.00	0.62	0.12	0.34
<u>Dugesia polychroa</u> ⁱ	.021	NS	0.37	1.24	3.32	1.84
<u>Planaria torva</u> ⁱ	.171	NS	0.32	1.53	4.71	2.46
<u>Polycelis tenuis</u> ⁱ	.106	NS	5.05	29.8	46.0	31.5

a from values on dominating bottom type; 0 or 1

b size < 50 mm

c size 50-150 mm

d size > 150 mm

e relative dominance score; 0 - 2

f $\mu\text{S/cm}$

g mg/l

h relative dominance score; 0 - 3

i absolute density per 30 min sampling

TABLE 2

Standardized canonical discriminant function coefficients

Variables	Discriminant function 1	Discriminant function 2
<u>Asellus aquaticus</u>	0.920	0.208
Mat-forming plants	-0.549	0.362
<u>Dugesia lugubris</u>	-0.232	0.930
Canonical correlation coefficient (R_c)	0.625	0.206

almost 94 % of the variation set by the given variables. The square of the R_c -value of the function can be interpreted as the proportion of variance in this discriminant function which is explained by the group attachment.

Fig. 2 shows the plot of all samples, using the two discriminant functions as axes. The group centroids, indicating the central position for the three groups, easily separate along the first discriminant function (all $p < 0.001$). Group 3 lakes contained least bottom vegetation and most A. aquaticus, whereas group 1 lakes showed the reverse. Group 2 lakes were intermediary as regards these two variables, but at the same time showed pronouncedly higher numbers of Dug. lugubris.

As a test of the adequacy of the discriminant functions derived, the computer program compared group membership of the lakes as assigned from the real density of D. lacteum with the predicted memberships, as derived from the discriminant functions, using the given variables. According to this procedure, 61 % of the lakes were correctly classified.

DISCUSSION

When studying the distribution of a species and relating the occurrence to different abiotic and biotic conditions, a restricted set of variables must be selected. The outcome of such an analysis can only in a simplified way indicate the crucial, and often more subtle, limiting factors in the complex ecology of a species. The variables selected to study must be rather constant

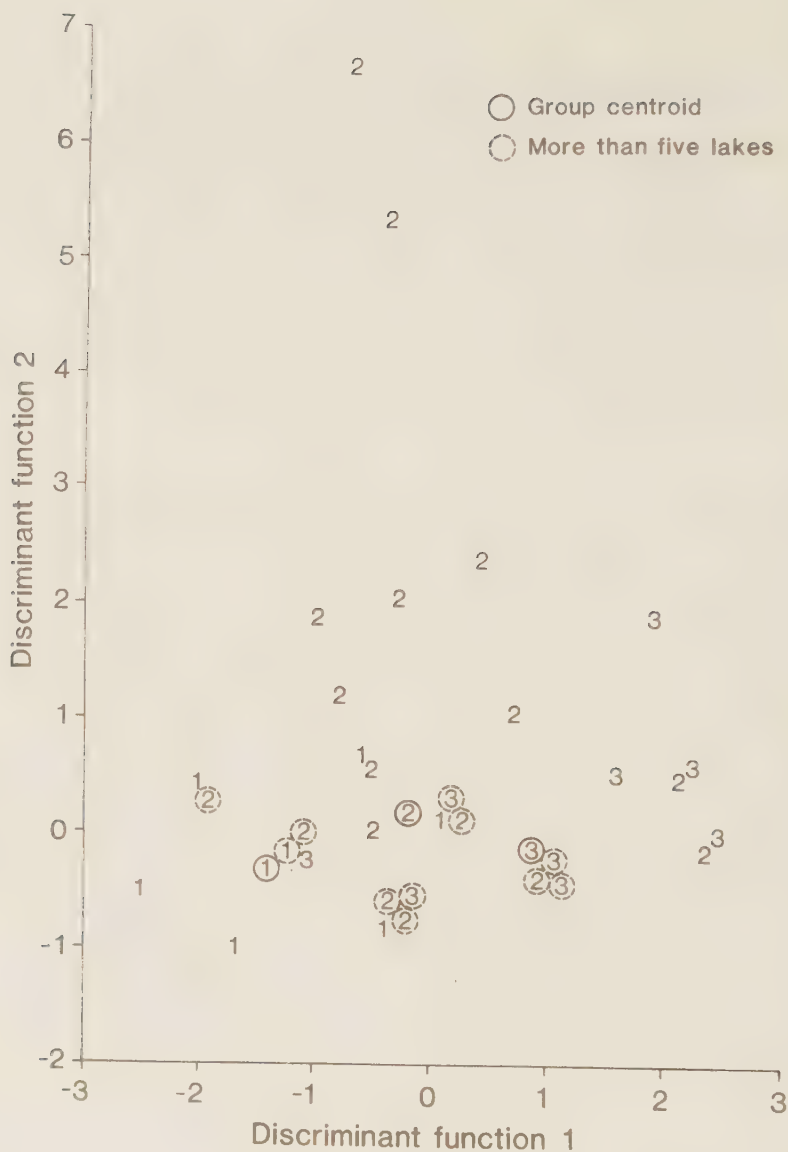


Fig. 2. Simultaneous scatterplot of all lakes along the two discriminant function axes. Each plot represents one or more lakes; plots for more than five lakes indicated. The figures indicate the (dominating) actual group membership of the lake(s).

or predictable over time as most sites can only be visited once or twice. A robust, bottom-dwelling species like D. lacteum is well suited for an analysis of this kind as short-time oscillations in e.g. oxygen and temperature seem of less importance. In this study, emphasis has been put on those variables more generally, and at the same time adequately, characterizing the different sites as well as the occurrence of the central prey item of D. lacteum.

Of the variables identified here, the abundance of the prey A. aquaticus turned out to be the most important factor explaining the distribution and abundance of D. lacteum. Previously, Reynoldson and Young (1966) and Økland (1980) have shown that D. lacteum and A. aquaticus often coexist. This reflects the fact that A. aquaticus forms the main prey item, "the food refuge", for D. lacteum (Reynoldson 1975, Herrmann 1982a).

According to Reynoldson (1966) most triclads prefer rather sheltered, stony shores. This was primarily not confirmed in the present study. However, when the analysis was restricted to nutrient-rich lakes, occurrence of D. lacteum was frequently correlated with prevalence of small stones in the habitat (see below). The occurrence of mat-forming plants (mainly charophytes, isoe-tids and low graminids) was generally important. The reason for this structural component affecting the density of D. lacteum negatively remains unclear.

The abundance of D. lacteum was found to be negatively correlated with that of Dug. lugubris. The main reason might be that Dug. lugubris almost exclusively occurs in eutrophic lakes (Dahm 1956, Reynoldson 1966, own unpublished observations), probably related to its dependence on gastropods as food (Reynoldson 1975). The present investigation did not involve any sampling of gastropods. However, a clear indication of their importance is the fact that the abundance of Dug. lugubris was strongest correlated with conductivity and calcium content ($r = 0.375$ and 0.316 , respectively, both $p < 0.01$).

In order to diminish the effect of the oligotrophic lakes, thus eliminating the irrelevant significant contribution by Dug. lugubris, as supposed above, a discriminant analysis on only those lakes ($n = 34$) characterized by either a conductivity of $> 200 \mu S cm^{-1}$ or a calcium content of $> 30 mg l^{-1}$ was carried out. The following parameters were now picked out as significantly promoting high D. lacteum densities; A. aquaticus (positively),

mat-forming plants (negatively) and small stones (positively), in mentioned order. The standardized canonical discriminant function coefficients became -0.948, 0.727 and 0.450, respectively, the value of R_c was 0.744 and 74 % of the lakes were correctly classified. Lakes with higher D. lacteum abundance were thus more often dominated by small stones.

As mentioned above, the relative abundance of A. aquaticus was the most important variable explaining high densities of D. lacteum. What conditions do then promote high A. aquaticus densities? Using simple linear regression analysis on the relation between the abundance of A. aquaticus and the environmental variables investigated, revealed highest correlation with conductivity ($r = 0.452$; $p < 0.001$).

Thus, of the factors available, the nutrient richness seemed best in predicting the density of A. aquaticus. This is probably due to an increased production of detritus and associated micro-organisms, mainly fungi (Rossi and Fano 1979). This is supported by Reynoldson and Young (1966) and Økland (1980), who, studying the distribution of A. aquaticus, stressed the importance of vegetation surrounding the lakes, especially the vegetation occurring sparsely around oligotrophic lakes in their regions. The same relation, via the amount of detritus, was reported for Gammarus lacustris Sars in a Norwegian high mountain lake with sparse shore vegetation (Larsson et al. 1978).

All types of lakes in the present study received much allochthonous material from the surroundings. In a number of British lakes with a calcium content $\leq 5 \text{ mg l}^{-1}$ studied by Reynoldson (1961) only 8 % contained A. aquaticus, while 89 % of the corresponding group of Swedish lakes did (this study). Maybe as a consequence, of lakes with $\leq 5 \text{ mg Ca l}^{-1}$ studied by Reynoldson (1966), only 2.5 % were inhabited by D. lacteum, while the corresponding figure drawn from the present data was 79 %.

Historical aspects, i.e. geographical barriers which may be overcome through time, seem to play an insignificant role for the present distribution of D. lacteum. It has been found in the conifer belt close to the Sarek mountains in northernmost Sweden (von Hofsten 1916) and is reported to occur even on the outskirts of the mountain area (Dahm 1956). The temperature regime may be a constraint in the distributional pattern (Reynoldson 1981, see also Herrmann 1982b) and partly explain the absence of D. lacteum in the interior of the northern high mountain region. The impact

of predation and parasitism on lentic triclads is generally regarded as negligible (Reynoldson 1981).

In sum, the distribution and abundance of D. lacteum seem primarily to depend on the occurrence of A. aquaticus, which in turn probably is governed by the productivity of the lake and its near-by surroundings via input of vegetation material. In the second place, the bottom structure plays a significant role, mainly through the inverse relationship to mat-forming plants. Also, an increased number of smaller stones (< 50 mm) seems to promote the presence of D. lacteum. The results seem plausible in the view of the knowledge of both the authors quoted above and myself. Hence, the results from the performed discriminant analysis provide a good explanation of the occurrence and abundance of D. lacteum.

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Population dynamics of *Dendrocoelum lacteum* (O. F. MÜLLER) (Turbellaria, Tricladida) in a South Swedish lake

By JAN HERRMANN, Lund

With 10 figures and 3 tables in the text

Abstract

Cocoon deposition, fertility, abundance, population composition and aggregation of a *Dendrocoelum lacteum* population were studied in a eutrophic South Swedish lake during two years, using artificial stones, and results were compared to British populations. Probably owing to intraspecific competition for *Asellus aquaticus*, the most important food, the adults shrank in spring and summer and eventually died off and were replaced by numerous young which grew rapidly during autumn. No distinct variations in energy and fat content throughout the year were found; probably triclads have no need for rapid energy mobilisation. Adults were found to contain more fat and energy than young, maybe in connection with cocoon production. The condition, mortality and reproductive potential are compared to British populations. The Swedish population of *D. lacteum* is suggested to be more of an r-strategist than the British one, because of more extensive temperature variations. Temperature, growth/maturation level and food are proposed to be the main factors in the reproduction phenology.

1. Introduction

The population ecology of several freshwater triclads has been studied in detail in Britain for decades by REYNOLDSON and his school (e.g. REYNOLDSON, 1958, 1966 a, 1975; REYNOLDSON & SEFTON, 1972). Thus the population dynamics of *Dendrocoelum lacteum* (O. F. MÜLLER) (Turbellaria, Tricladida), the subject of the present study, has been investigated by YOUNG (e.g. REYNOLDSON & YOUNG, 1963; REYNOLDSON et al., 1965; YOUNG & REYNOLDSON, 1966) in a small pond near Bangor, Wales. Recently, the relationship between *D. lacteum* and its chief prey, *Asellus aquaticus* L., has been examined in the stony littoral of Lake Windermere in northern England (WETTEWE, 1974; DE SILVA, 1976 a, b).

Basic taxonomic and ecological information on several triclad species in Scandinavia was gathered by DAHM (1958, 1961). Apart from his work, which does not treat the population ecology of *D. lacteum*, nothing has been published on the ecology of these animals in Scandinavia.

The present paper reports on the population ecology of *D. lacteum* in a small lake in southern Sweden. Special attention was directed towards annual variations in relative abundance, population composition, reproduction, growth and physiological status of the animals. Where possible, comparisons have been made with the same species' population dynamics in Britain, where climatic conditions are less severe than in Sweden and where the set of triclad species syntopic with *D. lacteum* also includes *Polycelis nigra* (O. F. MÜLLER), apparently absent in Sweden but rather common in the rest of Europe. This latter species might in some circumstances interact with *D. lacteum*, which therefore has a different competitive environment in Britain compared with Scandinavia.

2. The study area

The relative abundance of triclad species in all lakes in the southern and middle part of the province of Skåne in southern Sweden was surveyed in the summer of 1973 (unpublished). From this knowledge, Lake Bysjön was picked as suitable for a thorough study of *D. lacteum*. The lake is small (0.12 km², 30 acres, longest axis 500 m), almost circular and eutrophic, situated in a sandy area in the middle of south Skåne, approx. 23 km east of Lund (55° 41' N, 13° 33' E). The altitude above sea-level is 21 m. The circular shape, with its deepest part (8 m) in the middle, indicates that it originated as a kettle (HUTCHINSON, 1957).

The drainage area covers only 0.8 km², and the lake has no apparent inlet. Nutrient rich water drains into the lake from the surrounding agricultural land. Due to water lowering projects in the last years of the 19th century, the small outlet carries water only at high water level conditions. The lake is dimictic with a marked thermocline in summer and winter, at least when ice-covered. The temperature was recorded in the littoral from February 1975 and onwards

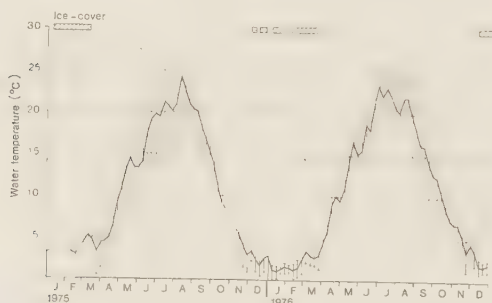


Fig. 1. Weekly average, maximum and minimum water temperature in the littoral of Lake Bysjön, calculated as an average of continuous recordings at 15 and 40 cm depth.

Table 1. Macroinvertebrates in the littoral of Lake Bysjön. The nomenclature is mainly in accordance with ILLIES (1967).

Tricladida	<i>Aeschna grandis</i> (L.) +
<i>Dendrocoelum lacteum</i> (O.F.M.) +++++	<i>Aeschna mixta</i> LATR. +
<i>Dugesia polychroa</i> (SCHMIDT) +	<i>Sympetrum</i> sp. +
<i>Polycelis tenuis</i> IJIMA +	
Nematomorpha	Hemiptera
<i>Gordius aquaticus</i> L. +	<i>Corixa</i> sp. +
Gastropoda	<i>Sigara falleni</i> FIEB. +++++
<i>Valvata piscinalis</i> MÜLL. +	<i>Ceris lacustris</i> L. ++
<i>Physa fontinalis</i> L. ++	<i>Ceris thoracicus</i> SCH. ++
<i>Galba truncatula</i> MÜLL. +	<i>Naucoris cimicoides</i> L. +
<i>Galba palustris</i> MÜLL. +	<i>Nepa cinerea</i> L. +
<i>Radix auricularia</i> L. ++	<i>Notonecta</i> sp. +
<i>Radix peregra</i> MÜLL. +	
<i>Lymnaea stagnalis</i> L. +++	Coleoptera
<i>Bathymophalus contortus</i> L. +	<i>Gyrinus</i> sp. +
<i>Gyraulus laevis</i> ALD. +++	<i>Haliplus confinis</i> STEPH. ++
Bivalvia	<i>Noterus crassicornis</i> MÜLL. ++
<i>Anodonta cygnea</i> L. +	<i>Hyphidrus ovatus</i> L. +
Oligochaeta	<i>Coelambus confluentis</i> F. ++
Tubificidae +++	<i>Hygrotus inaequalis</i> F. +
Lumbriculidae +++	<i>Rhantus exsoletus</i> FORST. +
Hirudinea	<i>Dytiscus marginalis</i> L. ++
<i>Glossosiphonia complanata</i> (L.) +++	<i>Enochrus testaceus</i> F. +
<i>Helobdella stagnalis</i> (L.) +++++	<i>Donacia</i> sp. +
<i>Theromyzon tessulatum</i> (O.F.M.) +	Megaloptera
<i>Hemiclepsis marginata</i> (O.F.M.) +	<i>Sialis lutaria</i> L. ++
<i>Piscicola geometra</i> (L.) ++	
<i>Haemopis sanguisuga</i> (L.) +++	Trichoptera
<i>Erpobdella octoculata</i> (L.) +++++	<i>Phryganea grandis</i> L. ++
Hydracarina	<i>Limnephilus flavicornis</i> FBR. +++
Not determined ++	<i>Limnephilus rhombicus</i> L. +
Crustacea	<i>Clyptotaelius pellucidus</i> RETZ. +
<i>Argulus foliaceus</i> (L.) +	<i>Athripsodes aterrimus</i> STEPH. +
<i>Asellus aquaticus</i> L. +++++	<i>Mystacides longicornis</i> L. +++++
<i>Gammarus lacustris</i> SARS +++++	<i>Molanna angustata</i> CURT. ++
Ephemeroptera	
<i>Cloëon dipterum</i> L. ++	Diptera
<i>Caenis robusta</i> ETN. +++++	<i>Tipula lateralis</i> MG. +
Plecoptera	<i>Ptychoptera</i> sp. +
<i>Brachyptera risi</i> MORT. +	<i>Chaoborus flavicans</i> (MEIG.) +
Odonata	<i>Chironomus plumosus</i> L. +++++
<i>Ischnura elegans</i> (LINDEN) +++	<i>Tanytarsus vernalis</i> G. +
	<i>Ceratopogon</i> sp. +
	<i>Stratiomyidae</i> +
	<i>Eristalis</i> sp. +
	<i>Notiphila</i> sp. +

Coarse classification: + = rare,
 +++ = common, +++++ = abundant,

++ = sparse,
 +++++ = very abundant.

using a Grant recorder equipped with two probes at 15 and 40 cm depth, respectively. Temperature data and duration of the ice cover are presented in Fig. 1.

Water close to the sediment surface in the littoral showed values for oxygen saturation ranging from 79–196 ‰, for Ca from 55–75 mg/l and for pH from 6.8–9.7. Further details about chemical and physical properties of the water are presented in COVENEY et al. (1977).

During winter an oxygen deficit period normally occurs, especially in the deeper parts, as a result of the degradation of dead organic matter and the respiration of the abundant fish stock. In some winters oxygen is depleted and hydrogen sulphide generates almost up to the ice-covered surface. Fish mortality, affecting especially the introduced rainbow trout (*Salmo gairdneri* RICHARDSON), has been known to occur under such circumstances. For further details see ANDERSSON & GELIN (1970).

Near the shore the bottom consists of sand with more or less detritus, and many stones of varying size. In the autumn large quantities of leaves fall into the lake from the surrounding fringe of trees, consisting mainly of elm (*Ulmus glabra* HUDS.) and alder (*Alnus glutinosa* L.). Under water deeper than about 2 m the bottom consists of a thick layer of fine soft mud.

The littoral flora is dominated by *Typha latifolia* L. and *Scirpus tabernaemontani* C. C. GMEL. Outside this zone *Potamogeton pectinatus* L. occurs commonly. Benthic macro-algae include *Spirogyra* sp., *Oedogonium* sp. and *Hydrodictyon reticulatum* (L.) LACERHEIM. The most abundant phytoplankton are *Sphaerocystis* sp., *Volvox* sp. and *Aphanizomenon flos-aquae* RALFS. The rate of primary production can change very drastically but generally remains high, so that the implanted fish stock, via zooplankton, grows very quickly. See also COVENEY et al. (1977), where also the zooplankton is dealt with.

Animals collected during the study period are listed in Table 1. The most abundant benthic species in the littoral were oligochaetes and chironomids, but also leeches, crustaceans and some insect species occurred in high numbers. The majority of taxa were most abundant on bottom under less than 1 m water, only *Chaoborus flavicans* (MEIG.) and sometimes chironomids preferring greater depth. A study of the effects of oxygen and hydrogen sulphide conditions on the bottom fauna in the deeper parts of the lake and the movements of *C. flavicans* was made in 1972 by WAHLSTRAND (1973).

3. Methods

3.1. Water analysis

By means of 20-ml syringes monthly water samples were taken from April 1974 to June 1975. Ca was titrated with Na-EDTA and pH measured on a Radiometer pHM 29. Oxygen values were obtained by precipitation in the syringe and titration with $\text{Na}_2\text{S}_2\text{O}_3$ (the micro-Winkler method).

3.2. Sampling

Monthly samples were taken from April 1974 to August 1976. Because of the strong preference of triclads to live under stones (hypopetrically), which occurred scattered over the soft bottom, an ordinary type of area-related sampling could not be used. Before January 1975, *D. lacteum* was only collected at random under stones, but this month 20 concrete bricks, measuring 20×40 cm, were placed with 8–10 m interval at about 30 cm depth. This method has earlier been

used by other triclad research workers, e.g. YOUNG & REYNOLDSON, 1966; REYNOLDSON & SEFTON, 1972. Calculations, following ELLIOTT (1971, p. 128), on different sampling occasions during the whole period showed that data from 10 to 18 bricks would be enough to provide a reliable picture of population events. Thus, from February 1975, it was also possible to estimate the relative density in addition to information about the population composition obtained in the earlier samples. The positions of the bricks were marked on the shore to facilitate their retrieval during the winter, when holes had to be cut through up to 20 cm thick ice.

The underlying supposition of course is that animals, irrespective of their size, neither prefer nor reject these artificial stones more than natural stones. According to control samples, taken in all phases of the triclad's life-cycle, the population composition was the same on natural as on artificial stones, except that the newly hatched individuals seemed to avoid all kinds of stones in their first weeks (see below). On each sampling occasion some animals were removed from the stones for further treatment in the laboratory. As *D. lacteum* was very abundant, this removal was not judged to affect the structure or size of the population. In addition to the information about *D. lacteum*, the bricks provided values for the variation in relative abundance of *A. aquaticus* and *Gammarus lacustris* Sars.

3.3. Population composition

The animals were taken to the laboratory, samples from different bricks being kept separate, where their length was measured by letting them crawl undisturbed in a petri-dish with some water over a millimetre graph paper. Each animal was dried by blotting it on a filter paper, placed on a preweighed cover-glass, dehydrated at 60 °C for 24 hours, and the cover-glass plus the animal was weighed to the nearest 0.01 mg on a Cahn Electrobalance. In this way the population composition in terms of both length and weight was assessed for each monthly sample.

3.4. Growth and shrinkage experiments

In order to estimate the potential growth of young *D. lacteum*, 25 newly hatched specimens with an average size of 2.58 mm were reared from 18 May to 9 June 1976 in lake water following lake temperature and given small crushed *A. aquaticus* as food. After these three weeks they showed an average length of 6.44 mm, thus having grown almost 4 mm.

Triclad are famous for their ability to withstand periods of starvation by shrinking, therefore an investigation of the shrinkage of *D. lacteum* during the critical period in the spring was also performed. On 23 April 1976 a set of 80 specimens was brought from the lake. Their lengths were determined, and the individuals were divided into two batches, as similar as possible in composition. The animals in batch 1 were individually dried and weighed, while those in batch 2 were starved in lake water with a natural temperature sequence to 4 June, when they were individually dried and weighed.

The average starting length and weight values in batch 1 were 16.13 mm and 4.06 mg, respectively, while animals in batch 2 were 16.21 mm. After the six weeks the values in batch 2 were 11.63 mm and 1.10 mg, respectively. Supposing the two batches could be considered identical, conclusions could be made about shrinkage in terms of both length and weight.

3.5. Physiological status of the animals

Animals and cocoons were analysed for energy content using the wet-oxidation method as described by WINBERG (1971). In total, 560 wet-oxidations from 30 sampling occasions during the period from April 1974–August 1976 were performed. As this method gives somewhat too low values, 36 measurements of the energy content of samples taken on five occasions were also performed using a microbomb calorimeter (PHILLIPSON, 1964), thus allowing a correction factor to be determined. On a few occasions during one year, animal samples were taken for determining ash content by muffle furnace combustion. Values for this were also calculated from the bomb calorimetry. Fat content was determined in 1975 according to the method described by SÖDERGREN (1973). All presented and discussed energy and fat values are related to ash-free dry weight (a f dw).

3.6. Cocoons

When cocoons were found, a certain number was taken to the laboratory, measured and transferred back to the lake, where they were put into glass jars, 5–10 cocoons in each, and checked once or twice a week. Thus the number of eggs and the hatching time of these cocoons under almost natural conditions could be calculated.

3.7. Determination of adults and terminology of ageing

In order to ascertain when and at what size the worms were functionally or potentially in the breeding stage, specimens collected over one year were sectioned and stained with Ehrlich's haematoxylin-eosin method. Considering as the main criteria the presence of sperm in the spermaducal vesicles and in the receptaculum seminis and the presence of numerous ripe ova in the ovary, the limits for being functionally or potentially reproductively active were put at 14 mm and 3.00 mg, respectively.

These limits were found to be reliable throughout the year except for a few animals of 14 and 15 mm size in the samples from June to October 1975 and 1976. Sectioned animals of these lengths from these months were, however, neither functionally nor potentially reproductively active. These animals were of adult length but thin and slim and of far from adult weight, and they prove that it is preferable to express the animals' condition and the population composition in terms of weight rather than length.

Thus, by "adults" is meant animals being 14 mm (or 3.01 mg) or more. By "young" is meant animals 1–4 mm (0–0.25 mg), inclusive. By "pre-adults" is meant the category 5–13 mm (0.26–3.00 mg), inclusive.

4. Results

4.1. Relative abundance

Because of the tendency of *D. lacteum* to spend its time almost exclusively on the underside of firm particles, mostly stones, the "artificial stones" (from now on called bricks) technique mentioned above could be used. This sampling technique does not allow the calculation of absolute numbers of animals. However, it is assumed that about the same proportion of animals is found under the bricks throughout the year, hence the

method is suitable for monitoring changes in population abundance and will give values of relative abundance. Fig. 2 shows the average numbers of *D. lacteum*, *A. aquaticus*, and *G. lacustris* per brick on the different sampling occasions.

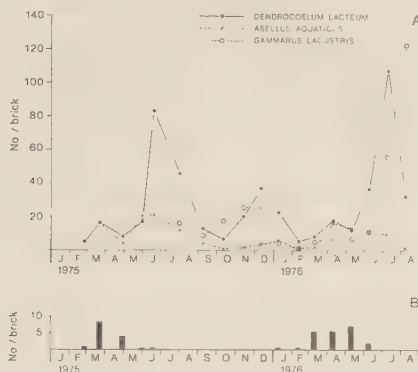


Fig. 2. A. Average numbers per brick of *D. lacteum*, *A. aquaticus*, and *G. lacustris*. Coefficient of variation mostly ranged from 45–90 %. — B. Average numbers per brick of cocoons of *D. lacteum*.

When the reproductive period of *D. lacteum* began in January–February, the population was sparse. In May the small newly hatched animals began to appear and produced marked peak abundances in late June until the beginning of July. In both years the peak abundances were about 18 times the lowest (in February). The population size then decreased again, but in November–December 1975 another lower peak was observed. The same trend could be traced in values from the autumn 1976, even if the sampling programme then was designed for other purposes and therefore did not show this change so clearly as in the previous year.

The numbers of *A. aquaticus* and *G. lacustris* did not show the same drastic seasonal change as *D. lacteum*. It seems, however, evident that the numbers of *A. aquaticus* increased in April–May, that is at the same time or somewhat before the peak of *D. lacteum*.

4.2. Reproduction

The average numbers of cocoons deposited under the bricks since the preceding sampling occasion (= one month) in 1975 and 1976 are presented in Fig. 2. Most cocoons were produced in March–April. More de-

tailed data on the cocoons from the 1976 breeding season are given in Table 2, calculated from subsamples of all cocoons deposited under the

Table 2. Cocoons (including sterile ones) deposited on the bricks during the reproductive period January—June 1976. The samples were taken on about the 10th each month.

Month	Total number of cocoons	Number reared	Average cocoon size	Hatched young/ cocoon	Total output of young
January	1	1	2.25	12.0	12
February	9	9	2.10	10.6	95
March	110	36	2.14	8.2	902
April	114	30	2.30	13.0	1482
May	142	41	2.19	9.6	1363
June	36	12	1.78	3.4	122
	412	129			3976

bricks. Because of the fact that the brick method was not introduced until the reproduction period had already begun and that the cocoon rearing procedure did not work properly, corresponding information from 1975 is incomplete. However, the same pattern seems to prevail both years.

The sequence of cocoon deposition only crudely reflects the time-course of reproductive output because the cocoons are known to contain

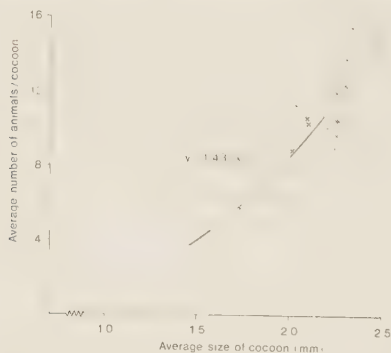


Fig. 3. Average number of animals/cocoon in relation to average size of cocoons in 1976. Sterile cocoons not included. Mostly n is around 10. In linear form, $r = 0.863$; $p < 0.001$.

very variable numbers of eggs and hence young triclads (from only a few up to about 50). A more accurate estimate of reproduction per time unit is obtained by counting the young triclads. Table 2 shows the number of animals/cocoon during the reproductive period of 1976 (January to June) based on counts of reared cocoons.

The figures above permit the calculation of the total output of hatched young. Most young hatched from cocoons deposited in a period from early March to early May. All the calculations include the cocoons that remained unhatched, i.e. were sterile. This category of the material made up 12%. A positive significant relationship between cocoon size and number of animals hatched, sterile cocoons excluded, was found, following a power function (Fig. 3).

To ascertain fecundity by counting the eggs in the female gonad is not possible as the ovary of *D. lacteum* contains eggs in all developmental stages, many of which are very small and impossible to count. Instead of fecundity the fertility is estimated in two ways:

- a) A relative measure of young triclads hatched is the number that would result from all cocoons found on the bricks during the whole season, taking into account the different numbers/cocoon. For 1976 this total number was 3976 (Table 2).
- b) Another relative measure is the number of pre-adults occurring on the bricks after the breeding period. The total number of 2145 specimens on the sampling date 7 July 1976 can be used for this purpose, as all animals at that time may be considered to originate from cocoons that hatched the same year.

The greatest problem remains: how many adults did produce this new generation? A relatively useful value can be obtained by the following method: The breeding season (the cocoon deposition phase) began in January; at that time (9 January 1976) 454 animals were found on the bricks. In June, when deposition ceased, most adult animals had died, most cocoons had hatched and the young animals had grown some millimetres. But there was a category of animals smaller than 14 mm, the adult limit (cf. 3.7.) but larger than 9 mm. This later length is taken to be the maximum size in June for the first animals hatching in April according to the growth experiments (cf. 3.4.). Thus, the 10–13 mm category on 8 June must have originated from the preceding year and probably did not take part in the reproduction in 1976. Consequently they must be subtracted from the January total. The remaining figure turns out to be 387 specimens.

These calculations yield two figures of fertility, viz. 10.3 young per adult and 5.5 young per adult, in both cases including also sterile cocoons. The first figure is probably too high, as the bricks are a particularly

favourable cocoon deposition place, and the latter probably too low, as some young animals die in their first weeks and also because the newly hatched animals to some extent seem to avoid the bricks. The true value is probably somewhere between these two.

4.3. Aggregation

The tendency of triclads to occur aggregated is well known (PEARL, 1903; REYNIERSE et al., 1969). The propensity for aggregation has been explained in terms of feeding strategy, i.e. the increased surface smeared with mucus, also used to facilitate the locomotion, when several individuals are involved may increase the probability for each individual to capture a prey (e.g. JENNINGS, 1957; REYNOLDS & YOUNG, 1963). Recently a thorough analysis of the importance of this behaviour for the ability of *D. lacteum* to capture its chief prey, *A. aquaticus*, and hence to grow, was conducted by DE SILVA (1976 a, b), who also took into account the size of the prey, alternative prey species, temperature, and substrate. The degree of crowding throughout the year, however, is an almost neglected question.

The brick samples were used to calculate the degree of aggregation. On all occasions the flatworms showed a highly contagious distribution (χ^2 -test, ELLIOTT 1971), i.e. in spite of the fact that the circumstances under every brick appeared similar, the animals were few under some bricks and numerous under others. The data fitted a negative binomial distribution.

LLOYD (1967) introduced the statistic $\bar{x}^*$, when presenting his „mean crowding“ model (Fig. 4). This statistic of course is strongly dependent of the value of $\bar{x}$, the mean abundance. Therefore he suggests using the ratio $\bar{x}^*/\bar{x}$ as a measure of the degree of patchiness. The relation to k in the negative binomial distribution is $\bar{x}^*/\bar{x} = 1 + 1/k$. ELLIOTT (1971) recom-

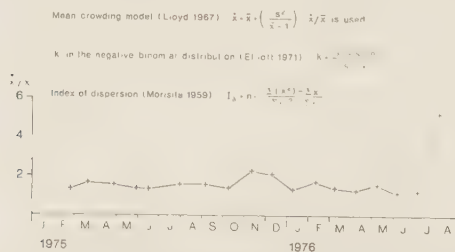


Fig. 4. Aggregation formulae and aggregation values of the brick samples, as calculated with the uppermost formula.

mends the reciprocal of k to measure the aggregation, while MORISITA (1959) earlier suggested a different "index of dispersion".

These latter two methods applied on my data gave essentially the same result as LLOYD's $\hat{x}/\bar{x}$. They were all used by GEORGE (1974) in a plankton distribution analysis, and he concluded that $\hat{x}/\bar{x}$ was the best index and that it was independent of $\bar{x}$ (confirmed by the present results, $r = -0.0189$; N. S.). The formulae for these three methods and the curve as calculated from $\hat{x}/\bar{x}$ are presented in Fig. 4.

4.4. Population composition and growth

As it was found difficult to obtain a repeatable length measurement of a triclad even when using the procedure described above, it was decided to describe the composition of the population of *D. lacteum* also in terms of weight (Fig. 5 a, b). However, the picture of the population is mostly

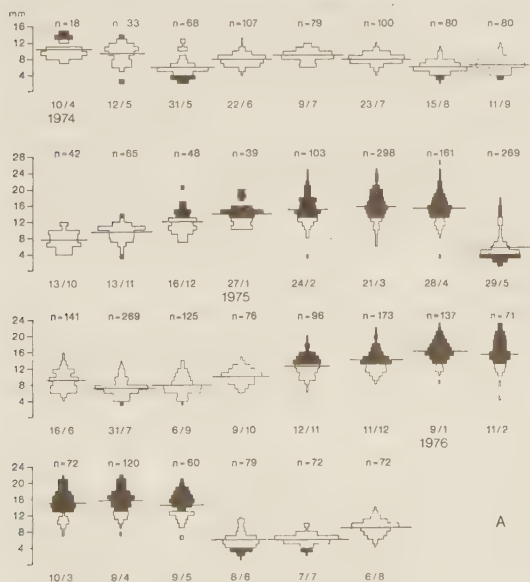


Fig. 5. A. Population composition in terms of length. Average values denoted by horizontal bars. Black areas indicate young and adult animals, respectively; the white areas in between are pre-adults. — B. As in A, but in terms of weight.

the same throughout the year, whether its composition is expressed in length or weight. The average individual weight for different months during an "average year" is presented in Fig. 6 a.

The change in weight over time can be expected to be proportional to the initial weight according to the general formula $dw/dt = k \cdot w$. The value of k , the growth constant, differs throughout the year and can be positive (growth), zero (no change), or negative (degrowth). Integrated, this gives the expression $(\log w_t - \log w_{t-1})/\Delta t$, where w_t = the weight at the end of the period, w_{t-1} = the weight at the beginning of the period and Δt = the length of the period.

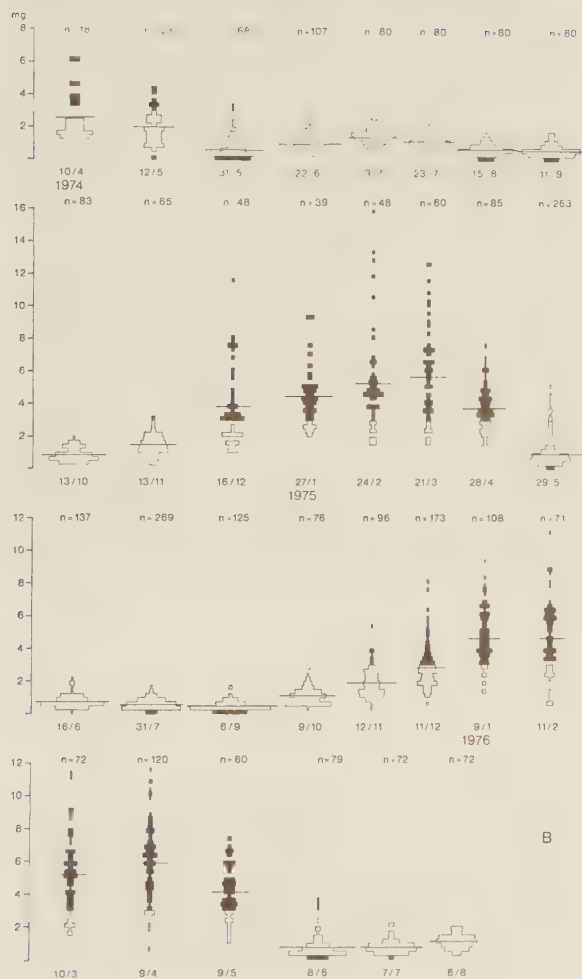
This expression is a measure of the relative growth, and since the growth is related to the size of the animal, it will more accurately indicate during which periods the animals put most effort into growth than will a comparison of absolute weight figures. From the graph in Fig. 6 a, values of the average individual's weight have been picked out on the 15th of each month and the animals' relative growth calculated as mentioned above.

In May—June numerous young animals appeared, resulting in a large majority of the worms weighing less than 1 mg (Fig. 5 b). These small specimens almost obscured the effect of a few still surviving adults, soon going to die off (Fig. 6 a). Though the two years were slightly different, they had in common that after a period of growth in the beginning of the summer, the average weight of the animals decreased for some weeks (degrowth). This pattern turns out the same irrespective of whether length of weight grouping is made (Fig. 5 a, b). An alternative interpretation of the data, in which the higher average weight figures in the middle of the summer are ignored, is given by the dashed line in Fig. 6 a.

The whole autumn was a long period of rapid growth (Fig. 6 a), resulting in most animals being adult when the winter began in December (Fig. 5 a, b). During the winter the average individual still grew, but at a lower rate (Fig. 6 a). This growing obviously is due to some individuals, at least, which increase more in weight than in length (Fig. 5 a, b).

In March—April a few individuals still were pre-adult. The heavier animals gradually disappeared (Fig. 5 a, b), causing a peak weight of the average individual in the population (Fig. 6 a).

During the period April—June the adults showed a rapid decrease in weight, length, and numbers (Fig. 5 a, b), also confirmed by observations from 1977, when the course of events was the same as in 1976 (Table 3). This fact combined with the appearing of a newly hatched triclad generation resulted in the rapidly descending curve of average weight (Fig. 6 a). This figure also presents the results of a shrinkage experiment (cf. 3.4.), indicating at what rate starving animals in the laboratory lost weight.



B

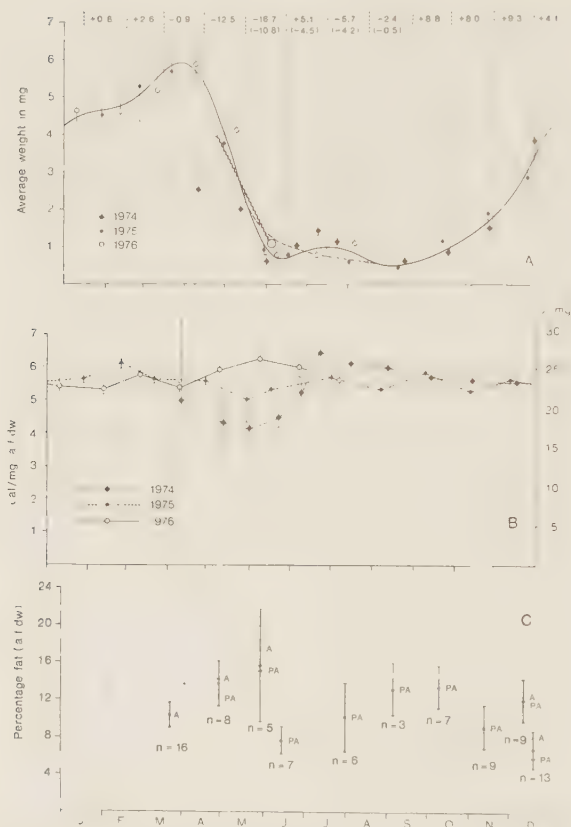


Fig. 6. A. The average individual dry weight throughout an average year. The curves are fitted by eye. Vertical bars indicate 95% confidence limits. The relative growth is given by the figures above, where those within brackets refer to the alternative dashed line. The descending wave line represents the shrinkage experiment presented in 3.4. Mostly $n = 60-140$. For further details see text. — B. Energy content. Vertical bars indicate 95% confidence limits. Mostly $n = 9-30$ (number of analyses). — C. Percentage fat (during 1975, except the last value which is from 1974). Vertical bars indicate 95% confidence limits. — A = adults, PA = pre-adults. n-values refer to number of analyses.

Table 3. Population events and condition during late spring 1977. The word "affected" denotes the animals being starved and probably shrunken, loose and white.

Date	Total number animals	Percentage adults	Condition
22 April	182	100	Good, well fed
7 May	96	100	c. 10 % of the adults affected
20 May	52	100	c. 50 % of the adults affected
3 June	261	c. 5	c. 90 % of the adults affected
17 June	2306	c. 0.1	100 % of the adults affected

If, for each sampling occasion, the average dry weight is plotted against the average length, one obtains Fig. 7. The best fit of these plots is a power (parabolic) function of the form $y = -2.12 \cdot x^{2.31}$, where x is the length and y the dry weight. In the linear form this has a correlation coefficient of 0.921. The regression coefficient for this relationship, 2.31, has got the 95 % confidence limits $= \pm 0.39$. This relation suggests an allometric growth relationship, typical for many animals and obviously also for flatworms in spite of their somewhat "elastic" length.

4.5. Physiological status

The variation in energy content of *D. lacteum* is presented in Fig. 6 b. The graph shows no distinctive seasonal tendency. Calculation of an average value of the energy content for *D. lacteum* during the whole per-

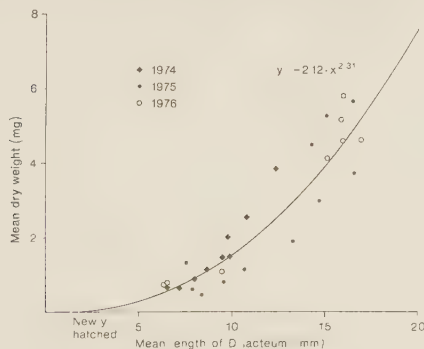


Fig. 7. Mean dry weight in relation to mean length of *D. lacteum*. In linear form, $r = 0.921$; $p < 0.001$.

iod resulted in 23.4 J/mg a f dw (ash-free dry-weight), using a micro-bomb calorimeter average correction factor of 1.08 and an average ash content value of 5 % (1 cal = 4.187 J). Energy content of the cocoons fell within the range from 21.8–24.5 J/mg a f dw and newly hatched animals contained 23.0 J/mg a f dw.

Using the limit for adults of 3 mg, energy content values for adults and pre-adults were calculated and compared for those occasions when both groups occurred, although two occasions had to be omitted because less than ten wet-oxidation analyses were available. The mean of the differences between pre-adults and adults in the tested comparisons is significantly different from zero ($p < 0.001$, $n = 13$; dependent t-test). Thus the adults were significantly richer in energy than were the pre-adults. The average adult and pre-adult values were 23.9 and 23.2 J/mg a f dw, respectively.

The fat content (Fig. 6c), like the energy content, shows little and indistinctive variation over the year. If the values for pre-adults and adults were separated on those four occasions when both groups occurred, the adults displayed significantly more fat than did the pre-adults, 13.0 % and 11.1 % (both a f dw), respectively ($p < 0.05$, $n = 4$; dependent t-test used as above). Fat content of cocoons was determined to 16.5 % (a f dw).

An alternative way of describing the condition of *D. lacteum* is to calculate, instead of energy or fat contents, the "expected weight" (cf. BAGENAL, 1957) for a given length. As a suitable length was chosen 10 mm, a size class always more or less frequent in the population. The calculations were made from the regression analyses made for each month on animals

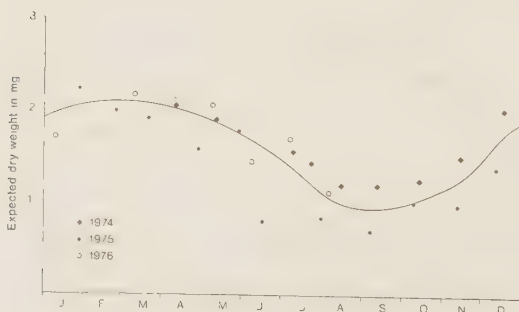


Fig. 8. Expected dry weight of a 10 mm long *D. lacteum*. The curve is fitted by eye.

measured both to length and dry weight (cf. 4.4.). The resulting 28 values are plotted against time in Fig. 8.

5. Discussion

Regulation is a central concept in population dynamics. From the data presented above certain interpretations are possible. For more definite conclusions concerning the regulating mechanisms and the triggers for the onset and termination of the reproduction it is, however, often necessary to perform laboratory experiments. The results of these will be published elsewhere.

5.1. Reproduction

D. lacteum deposited cocoons from January to June (inclusive). During this period the temperature ranged from 1 °C—20 °C (weekly average values). This agrees with the laboratory experiments of REYNOLDSON et al. (1965), who found *D. lacteum* capable of producing cocoons in a temperature range of at least from 1.5 °C—18.5 °C, but not at 23 °C. After sectioning specimens reared at 1.5 °C to produce cocoons they concluded, however, that *D. lacteum* only rarely was able to do so at that temperature. In contrast to this, the population in Lake Bysjön normally produced a lot of cocoons in spite of such a low temperature (Fig. 1 and 2).

As every cocoon contained numerous eggs and hence young animals and there was a positive relation between cocoon size and animals/cocoon (Fig. 3), the size of the cocoons is considered to be perhaps as important as the number of cocoons deposited for the total reproductive success, i.e. the total output of young. In the samples from 1976, this leads to a difference (Table 2): while the number of cocoons culminated in the May sample (mainly deposited in April), the highest monthly output of young occurred from the cocoons obtained in the April sample.

In Britain as well as in my study area the peak of cocoon abundance fell when the temperature was about 8—12 °C. Cocoon deposition ceased at 17—20 °C, although this temperature is reached in June in Sweden but not until August in Britain.

YOUNG & REYNOLDSON (1966) estimated the fertility at 4.9—6.9 young per adult, depending on the calculation procedure, but in both cases not taking into account the sterile cocoons. My calculations gave 5.5—10.3 young per adult (cf. 4.2.), also depending on the calculation procedure. The Swedish population obviously possessed a higher reproductive potential, a property that will be commented on below. It was more successful also in having only 12 % sterile cocoons, as compared to 19 % (WETTEWE, 1974) and 34 % (YOUNG & REYNOLDSON, 1966) in Britain. The last value

leads to an even lower fertility in the population investigated by YOUNG & REYNOLDSON (1966), and this is the figure to be compared with the fertility in the population in Lake Bysjön.

5.2. Life cycle

The cocoon deposition of *D. lacteum* culminated in late April (Fig. 2). Under natural conditions the water temperature rises from 7 °C to 13 °C during the following weeks, and under this regime incubation time is on average about 35 days (unpublished data, also REYNOLDSON et al., 1965). Consequently hatching will culminate in late May. The size of a newly hatched *D. lacteum* is on average 3 mm (ranging from 1.5 to 4 mm). According to the growth experiments in the laboratory the young worms increase by almost 4 mm during their first three weeks (cf. 3.4.). This calculation leads to an expected average size of almost 8 mm in late June, and as the old individuals are very few by then, the cohort of young and small pre-adult animals is expected to make up the greatest part of the population.

These calculations from my laboratory experiments are all in good agreement with the situation observed in the field. However, it is clear that the newly hatched individuals are missed with the brick method. They obviously avoid the bricks during their first month or so, and very few of these thin white worms ≤ 4 mm were ever found in spite of many cocoons being deposited underneath the bricks, which obviously were preferred for this purpose. The same situation was also true for natural stones in the lake. Thus, the newly hatched worms became underrepresented in the samples and hence the total numbers during the large peaks (Fig. 2) were even larger in reality.

In their study of the population of *D. lacteum* YOUNG & REYNOLDSON (1966) used both the brick method and a quadrat method. With the latter technique a certain area of the leaf-covered pond bottom was sampled. The quadrat method was shown to have a consistent tendency to yield proportionately more young specimens.

The numerical increase of the category between newly hatched and adults, called pre-adults, from May to July, was thus caused by migration to the stones by young triclads. Their growth in combination with shrinkage of the dwindling number of adults (Table 3) caused a successive concentration of the population in terms of size distribution (Fig. 5 a, b).

The abundant occurrence of small (2–5 mm) *Asellus aquaticus* in June–August allowed rapid growth of the small *D. lacteum*, and the average weight of the latter increased up to a distinct summer peak (Fig. 6 a). Since the abundance estimates for *A. aquaticus* from the bricks are crude

and, moreover, give no information about the size composition, information from a thorough study of the population dynamics of *A. aquaticus* in the nearby Lake Håckebergasjön has been used (F. FRIBERG, unpublished) on the justifiable assumption that the course of events probably was fairly similar in the two lakes.

The number of *A. aquaticus* began to decrease towards August (Fig. 2), may be partly because of predation by *D. lacteum*. The number of *A. aquaticus* began to drop when *D. lacteum* reached its peak in June. This fact combined with the fast growth of *D. lacteum* probably led to intraspecific competition in the *D. lacteum* population, resulting in prolonged shrinkage and finally to the death of some pre-adults of all sizes (the down slope in the summer peak in Fig. 6 a).

After these changes in the population the remaining individuals of *D. lacteum* exhibited a rapid growth during the autumn (Fig. 6 a), facilitated by the growing *A. aquaticus* (F. FRIBERG, unpublished). They may also feed on *Gammarus lacustris*, but probably to a lesser extent since this species is more difficult for the worms to entangle (unpublished). The high number of *G. lacustris* during the summer 1976 cannot be coupled with any event in the *D. lacteum* population and this remains unclear.

The peak numbers of *D. lacteum* on the brick samples in November—January (Fig. 2) of course were not a result of new animals being added to the population, since the hatching period ceased in late June, but of some kind of migration, maybe from the bottom level nearest to the shore so as to avoid the risk of being caught in the ice. They do not, however, migrate to deeper water than 1.5 m, an observation also supported by BERG (1938), and usually remain in still much shallower water.

Supposing that the bricks were favourable sites for *D. lacteum*, the peak could also be a result of an increased aggregation tendency during this time of the year as shown in Fig. 4. The advantages of aggregation may be two: first, the triclads benefit from "cooperating" when snaring the numerous prey needed for their rapid growth (Fig. 6 a), and second, the first phase of the breeding period, the copulation, commences at about this point, resulting in the onset of cocoon deposition in January—February (Fig. 2). WETTEWE (1974) compared the degree of aggregation for *D. lacteum* in March, July, and November and also found the highest crowding tendency in November.

Adult worms were virtually absent during the summer but made up 80—90 % of the population in January—March (Fig. 5 a, b). The relative growth rate was highest in October—December, which might seem remarkable as the temperature was by then steadily decreasing. REYNOLDS et al. (1965), however, demonstrated that the growth rate of *D. lacteum*, as opposed to other triclads, is high even in water colder than 10 °C. The re-

lative growth rate decreased in January—March, but was still positive (Fig. 6 a). At this time the temperature was 1—2 °C.

In March the ice broke up, beginning along the shore, the temperature rose (Fig. 1), and the activity of *D. lacteum* increased. This resulted in more triclads moving to the bricks to deposit cocoons. This process was at its maximum in April (Fig. 2), thus coinciding with the maximum proportion of adults in the population (Fig. 5 a, b) and with the peak of average weight (Fig. 6 a). Combined calculations from Figs. 2 and 5 a, b show that during April—May the absolute number of adults diminished, probably mainly owing to mortality, because the numbers of pre-adults remained the same.

During April—June the average weight of the worms fell drastically (Fig. 6 a). The shrinkage experiment, the result of which is demonstrated in Fig. 6 a and which was conducted at the same time, presumably represents the maximum shrinkage potential under field conditions. This is, however, far from enough to explain the drop in size of the average individual, and a relatively high death rate of adults must have prevailed. As a result, in June an almost complete substitution of the old by the new generation had been performed. The occurrence and the relatively high rate of these events were also found in 1977 (Table 3).

5.3. Energy and fat contents

Many invertebrate species store energy, often in the form of fat, during the months preceding the reproduction, for example to facilitate a rapid production of numerous offspring. If this is the case in *D. lacteum*, peak values of energy and fat content would be expected to occur during January—March. However, no such peaks were revealed neither by the energy nor the fat analyses performed (Fig. 6 b, c). Perhaps *D. lacteum* should not be expected to store plenty of energy since the reproductive period covers several months, during which food scarcity probably does not prevail. Moreover, triclads of course do not need energy reserves for the energy-demanding metamorphosis characteristic of insects.

The overall energy content of 23.4 J/mg found in this study is rather high compared to most invertebrates, but CALOW & JENNINGS (1974) obtained an even higher value, 26.4 J/mg, for *D. lacteum*, and numerous measurements for other triclads also gave relatively high values. This is perhaps not so surprising considering the fact that triclads contain no endo- or exoskeleton, which are mostly low energy tissues, but mainly consist of muscles.

On average, adults showed significantly higher fat and energy levels than did pre-adults. This might be explained by the relatively high fat content in the cocoons, which may also be expected to result in high fat

contents in newly hatched animals compared to larger ones. This was found by CALOW & WOOLHEAD (1977) under experimental conditions.

My energy analyses of cocoons and newly hatched animals were both similar to the overall average value for the whole population. In agreement with my findings, CALOW & WOOLHEAD (1977) reported only minor differences in energy content between newly hatched and larger animals. All their values were, however, higher than mine, probably because their animals were provided with food in superabundance.

The fat values from Lake Bysjön seem to be relatively low, at least compared with results in the study of the triclad *Dugesia tigrina* (GIR.) performed by BODDINGTON & METTRICK (1971). According to the same authors fat is not very important for triclads as an energy reserve. From their analyses they propose lyo-glycogen as being more important, which is somewhat surprising as its energy value is not higher than that of most other carbohydrates. CALOW & WOOLHEAD (1977) reported a marked decrease by percentage of both lipids and carbohydrates in degrowing *D. lacteum*. The strategy for storing energy may well differ within a species or a group, depending on the environment (DERICKSON, 1976).

5.4. Regional comparisons of reproductive strategies

For *D. lacteum* from Lake Windermere, DE SILVA (1976 a) established a very close correlation between length and dry weight. An interesting difference is that the regression coefficient was significantly ($p < 0.01$; BAILEY, 1959, p. 98) higher in her than in my population (3.07 and 2.31, respectively) (Fig. 9). This means that an animal with a certain length weighs more in Lake Bysjön than in Lake Windermere. A possible inter-

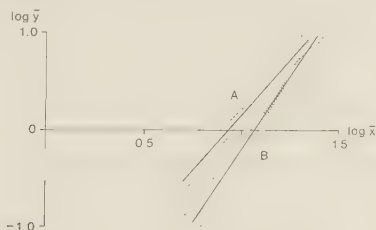


Fig. 9. Comparison of regression coefficients (slope values) and the position of regression lines for the regression of log average dry weight (y ; in mg) on log average length (x ; in mm) for *D. lacteum*. A = the population in Lake Bysjön; Fig. 7 in linear form. B = the population in Lake Windermere; calculated from WETTEWE (1974) and DE SILVA (1976 a). The dashed and pointed lines indicate the 95% confidence limits.

pretation is that *D. lacteum* generally is in a better condition in Lake Bysjön than in Lake Windermere, possibly because it suffers less from competition. This is a quite plausible explanation, since *D. lacteum* is the only triclad in Bysjön, while in Lake Windermere there are several species that are known to compete for food (REYNOLDSON, 1975).



Fig. 10. Comparison of the average individual dry weight throughout an average year between Lake Bysjön (A) and Lake Windermere (B).

From diagrams of the population composition presented by WETTEWE (1974) and the regression line in DE SILVA (1976 a) a curve of the average individual weight in the Windermere population was calculated and compared to the corresponding curve in this study (from Fig. 6 a) in Fig. 10. They follow the same general pattern, except for the striking difference that the annual cycle from Britain is about one month earlier. This might be explained by the difference in temperature regimes. The lowest and highest temperature values are more moderate in Britain, thus allowing the animals to put more energy (effort) into growing instead of into evasion from or physiological adaptations to the dangerous temperatures. Higher temperature in itself also allows higher metabolic rate, and thus an earlier development of reproductive organs.

YOUNG & REYNOLDSON (1966) performed their study of *D. lacteum* in a pond in Wales, where the temperature regime was similar to that of Lake Windermere, average values ranging from 5–15 °C. Both these populations showed smaller fluctuations in total population numbers than did the Swedish one (peak values 4 and 18 times the bottom values, respectively). A comparison of the abundance figures in Fig. 2 with those of YOUNG & REYNOLDSON (1966) and of WETTEWE (1974) reveals that especially the latter author found the peak values for *D. lacteum* to occur later in the summer.

The population composition throughout the year seems to be roughly the same in Sweden as in Britain, but YOUNG & REYNOLDS (1966) suggested that about 40 % of the animals of the population survived their first summer and thus became two years old. In the population in Lake Bysjön all facts indicate that practically all specimens became only one year old. This difference can be explained by the rapid shift in population composition. Temperature rises faster in Lake Bysjön than in the pond in Wales, young animals grow faster and utilize the food present. The adult specimens do not manage to compensate for this enhanced intraspecific competition by shrinking fast enough, so they die. In line with this, REYNOLDS (1966 b) showed that young triclads survived better than shrunken adults in case of food shortage.

BODDINGTON & METTRICK (1974) investigated the population dynamics of the triclad *Dugesia polychroa* (SCHMIDT) in Canada and compared the results to a study of the same species in Britain made by REYNOLDS (1961). The climatic differences were very similar to those between South Sweden and Wales, and it is interesting to note their report of the same population differences in the amplitude and speed of the population fluctuations as well as in the adult mortality.

The more extreme temperature values, the speed of change between these, and the proposed effects of this regime, suggest that Lake Bysjön is a more severe environment than the British localities. This causes a more pronounced tendency of periodic reduction of the *D. lacteum* population in Lake Bysjön, and this in turn makes a high output of offspring selectively advantageous. As noted in 5.1., the fertility of the Swedish population is noticeably higher than that of one of the British populations. In other words, the Swedish population of *D. lacteum* seems to have adopted more of an r-strategy than the British populations with which it is being compared. By this reproductive tactic, it maximizes its reproductive value (PIANKA, 1976).

6. Concluding remarks

The fitness of an individual is proportional to its adaptedness to the environment. The more fit an individual is, the more easily can it convey its properties to the next generation in the form of more descendants (PIANKA, 1974). An important component of the mentioned adaptedness is the reproductive phenology, and an interesting question is what stimuli start and stop the reproductive activity in *D. lacteum*.

A necessary qualification is that the copulatory organs are well developed and that gametes are produced. From the sectioning (cf. 3.7.) I know that the first specimens of *D. lacteum* to show these properties did not appear until November, thus enabling copulations to begin. The first

cocoons were deposited in January (Fig. 2), although the majority were not deposited until later, probably because of the period of cold temperature beginning in December. The growth and maturation is retarded by this regime (Fig. 6 a, see also REYNOLDSON et al., 1965; WETTEWE, 1974).

Since no marked temperature rise was recorded until March, but *D. lacteum* started cocoon deposition much earlier, temperature per se seems not to be the proximate releaser. More likely, temperature in terms of degree-days combined with the initial stage of growth of each animal mediates the maturation time of the animal, provided that prey animals are present. This last important prerequisite was demonstrated by WETTEWE (1974) in an elegant experiment.

As newly hatched *D. lacteum* appeared in the littoral of Lake Bysjön in May—June, the entire population entered a stage of increasing intra-specific competition for the declining numbers of *A. aquaticus*, which form the preferred food. This competition is indicated by the fact that the number of *A. aquaticus* decreased as the number of *D. lacteum* increased, the latter probably having a direct impact on *A. aquaticus*. The same time-lag between the abundance peaks of the prey and the predator was found also by WETTEWE (1974), while YOUNG & REYNOLDSON (1966) found them to coincide.

The gradually aggravated food shortage impaired the condition of *D. lacteum* and caused difficulties for the worms to endure the high temperatures in the summer, so they degenerated and died off (Table 3). However, already in advance of this difficult period, some individuals had stopped breeding, so the reproductive termination probably is affected also by the age of the animals, in other words, endogenously. That competition for food is severe in spring and summer is further supported by Fig. 8, showing that the worms were then in a relatively poor nutritional condition.

No trace of interspecific competition between *D. lacteum* and any other carnivore has been detected, as there is no other serious predator on *A. aquaticus*. According to DAVIES & REYNOLDSON (1971), predators and parasites have little impact on *D. lacteum*, and my field experience is the same. These circumstances indirectly support my conclusion that the population dynamics of *D. lacteum* in Lake Bysjön is strongly affected by periodic food shortage, i. e. intraspecific competition.

Summary

Population dynamics of a dense population of *Dendrocoelum lacteum* in a small eutrophic lake in southern Sweden, with large temperature fluctuations during the year, was studied during two years. Because of the strong preference of the animals to live hypopetrically, artificial stones were used during most of

the investigation period. These proved to give realistic samples at all times of the year, except that newly hatched animals were under-represented. The sampling method provided values of the relative abundance of *D. lacteum*, *Asellus aquaticus* and *Gammarus lacustris* (Fig. 2). The triclads were examined in terms of length and dry weight as well as of energy and fat content. On the basis of sectioned specimens from the whole year, the limits for being adult were put at 14 mm or 3 mg, respectively.

Cocoon deposition occurred from January—June, but most cocoons were deposited during March—April (Fig. 2), coinciding with a temperature of around 10°C, with maximum abundance of adults, and with maximum average length and weight of the adults (Figs. 5 a, b, 6 a). The fertility varied between 5.5 and 10.3 young per adult, depending on the calculation procedure. In May—June numerous young hatched, eventually causing intraspecific competition for the preferred food, *Asellus aquaticus*, and this led to the death of many pre-adults. The adults, probably being susceptible to food shortage combined with high temperatures, shrank and died off, thus becoming only one year old. The growth during the autumn and winter culminated in November—December, in spite of the cold water (Fig. 6 a). During this period aggregation increased, either because of the great need of food for growth or because of the beginning sexual activity (Fig. 4). Growth of *D. lacteum* probably is allometric (Fig. 7).

D. lacteum, like other triclads, contains a small portion of low energy tissues, and was found to have relatively high energy but low fat content. Throughout the year variations in energy and fat content were small (Fig. 6 b, c), and perhaps triclads have little need for rapid energy mobilisation. However, adults were found to contain more energy and fat than young worms, which probably has to do with cocoon production.

The condition of the population of *D. lacteum*, in terms of the regression coefficient for the correlation length/dry weight, was found to be superior to that of a British population, maybe because of differences in the strength of interspecific competition (Fig. 9). The British population performed its growth and degrowth some weeks before the Swedish one, probably as a consequence of different temperature regimes (Fig. 10).

In contrast to British adult triclads, the Swedish adults very rarely, if ever, survived for more than one year. The facts that more young are produced, that the newly produced young grow more rapidly and that they, according to British observations, are more capable to withstand periods of food scarcity than the adults, are suggested to explain this difference. The reproductive potential and the variations in population size are higher in Sweden. The onset and termination of the reproduction activity of *D. lacteum* are supposed to depend on combinations of 1) temperature, 2) growth/maturation level, and 3) availability of food.

Hence, the Swedish population inhabits an environment which promotes the evolution of more pronounced r-strategist features than were found in the British populations available for comparison.

Zusammenfassung

In einem kleinen südschwedischen, eutrophen See mit großen Temperaturschwankungen wurde die Populationsdynamik eines dichten Besatzes von *Dendrocoelum lacteum* während zweier Jahre untersucht. Da die Tiere sich vorzugs-

weise unter Steinen aufhalten, wurden zum größten Teil während der Untersuchungsperiode künstliche Steine verwendet. Die nach dieser Methode erhaltenen Proben entsprachen der natürlichen Verteilung während des Jahreszyklus. Nur waren neugeschlüpfte Tiere unterrepräsentiert. Die hier angewandte Sammelmethode gab über die relative Abundanz von *D. lacteum*, *Asellus aquaticus* und *Gammarus lacustris* Aufschluß (Fig. 2). Länge, Trockengewicht, Energie- und Fettgehalt der Trikladen wurden bestimmt. An Hand von Schnittserien (ganzer Jahreszyklus) wurde das Stadium der Geschlechtsreife auf die Länge von 14 mm und das Gewicht von 3 mg festgelegt.

Bei einer Temperatur von 10 °C wurden Kokons in der Zeit von Januar bis Juni abgelegt, die meisten jedoch im März–April (Fig. 2). In dieser Periode war auch die Zahl der geschlechtsreifen Tiere am höchsten, es gab die längsten und schwersten Tiere (Figs. 5 a, b, 6 a). Je nach der Methode der Berechnung schwankte die Fertilität zwischen 5.5 und 10.3 Jungen per geschlechtsreifem Individuum. Im Mai und Juni schlüpften die Jungen massenhaft. Das führte zu intraspezifischer Konkurrenz bei der Suche nach der beliebtesten Nahrung, *Asellus aquaticus*, und zum Absterben vieler Präadulten. Da Nahrungsmangel und hohe Temperatur gemeinsam die geschlechtsreifen Tiere negativ beeinflussen, wurden die Individuen immer kleiner und erreichten nur das Alter von einem Jahr. Trotz der tiefen Wassertemperaturen kulminierte das Wachstum im November–Dezember (Fig. 6 a). Während dieser Zeit aggregierten die Tiere auch mehr, vielleicht wegen des großen Nahrungsbedarfs oder der beginnenden Sexualität (Fig. 4). Wahrscheinlich ist der Körperzuwachs bei *D. lacteum* allometrisch (Fig. 7).

Wie andere Trikladen, enthält *D. lacteum* wenig niedrigerenergetisches Gewebe und wies einen relativ hohen Energiegehalt, jedoch einen relativ niedrigen Fettgehalt auf. Die Variationen in Energie- und Fettgehalt im Jahreszyklus waren unbedeutend (Fig. 6 b, c). Vielleicht ist bei Trikladen der Bedarf an schneller Energiemobilisierung nicht groß. Bei geschlechtsreifen Tieren erwies sich jedoch der Energie- und Fettgehalt größer als bei jungen Tieren, was wahrscheinlich mit der Kokonproduktion zusammenhängt.

Der Regressionskoeffizient der Korrelation zwischen Länge und Trockengewicht wurde als Maß der Kondition der *D. lacteum* Population verwendet. Es stellte sich heraus, daß diese besser war als die Kondition einer englischen Population, was auf der unterschiedlichen interspezifischen Konkurrenz beruhen kann (Fig. 9). Der Körperzuwachs in der englischen Population erfolgte einige Wochen vor dem in der schwedischen Population. Das beruhte wahrscheinlich auf den unterschiedlichen Temperaturverhältnissen (Fig. 10).

In Schweden überleben im Gegensatz zu England geschlechtsreife Tiere selten, wenn überhaupt, mehr als ein Jahr. Dieser Unterschied könnte dadurch erklärt werden, daß mehr Nachkommen produziert werden, daß die Neugeschlüpften schneller wachsen und daß diese, wenigstens in England, einen Nahrungsmangel besser überleben können. Die Populationsgröße variiert in Schweden mehr und das Reproduktionspotential ist hier auch höher. Der Anfang und das Ende der Reproduktionsaktivität von *D. lacteum* sind vermutlich von 1. der Temperatur, 2. dem Zuwachs- und Reifenniveau und 3. dem Nahrungsbestand abhängig.

Somit fördert das Milieu der schwedischen Population die Entwicklung von stärker betonten r-strategischen Zügen mehr als das der mit ihr verglichenen englischen Population.

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510 J. Herrmann, Population dynamics of *Dendrocoelum lacteum*

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REPRODUCTIVE PHENOLOGY IN DENDROCOELUM LACTEUM (TURBELLARIA)

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The triclad Dendrocoelum lacteum and its cocoons were reared under natural lake conditions in the laboratory. Hatching time for cocoons was found to depend on temperature as an inverse power function. Estimated required degree-days was 266. Cocoon deposition culminated in late April, peak of hatchling occurrence was two weeks later. Hatchlings per cocoon and cocoon viability declined as spring proceeded. Cocoon deposition ceased in June because of deteriorating adults. Newly hatched triclads avoided stones for some weeks. All results were compared with British ones. Earlier reproductive performance with higher output levels were found in Sweden. I suggest this could be attributed to: 1) better food availability, producing larger triclads and thus higher reproductive potential, and 2) faster increase in temperature during spring, thus also avoiding high summer temperature, which are vulnerable to early developmental stages.

INTRODUCTION

Dendrocoelum lacteum (O.F. Müller), the most wide-spread triclad in Europe (Dahm and Gourbault 1978), inhabits a large variety of fresh-water habitats. Because of different abiotic and biotic conditions within its distributional area there are good reasons to expect considerable regional differences in its biology. Important aspects of this include responses to different temperature regimes, to different prey availabilities, and impact of presence or absence of competing species.

The dynamics of populations of D. lacteum in Great Britain was studied by Young and Reynoldson (1966) and Macan and de Silva (1979). A South Swedish lake population was found to differ from the British ones (Herrmann 1979). The most conspicuous features of the former population were 1) that the total animal abundance peak occurred earlier in the year, 2) that fertility and viability appeared higher, and 3) that the highest average weight values of the animals seemed to occur somewhat later in the spring.

Laboratory experiments have demonstrated that Asellus aquaticus L. is the main food for D. lacteum in England as well as in Sweden, and also that increased food supply increases the reproductive output (Herrmann 1982a). In the present study the reproductive output of animals reared in the laboratory and of a lake population are presented. In other experiments the importance of temperature as a trigger for the reproduction events has been investigated (Herrmann 1982b).

MATERIAL AND METHODS

All cocoons and adults used in the present study were collected

in Lake Bysjön ($55^{\circ}41'N$, $13^{\circ}33'E$), described in detail by Herrmann (1979). Some cocoon incubations were performed in 1976, all other data are from 1977. It was considered that the collecting of triclads and cocoons from the lake could only have a very marginal influence on the D. lacteum population.

Cocoons newly deposited and collected were incubated in glass tubes at 5° , 10° , 15° and $20^{\circ}C$, respectively, and hatching time was recorded. Further treatment of these data is presented below.

Adult triclads (≥ 14 mm) were collected from March through to June and sectioned as described in Herrmann (1979). Presence of sperm in the spermiducal vesicle and ova in the ovary were used as criteria for determining whether an animal was in the reproductive state.

The reproduction of a natural population of D. lacteum was studied in two ways:

A. Laboratory-produced cocoons (LP). 40 adults of reproductive size (≥ 14 mm) were collected at intervals of 2 weeks from 1 February to 1 June, thus representing the entire reproductive season. A very small number of cocoons might have been deposited in January. The triclads were reared in jars supplied with recirculating, thermostatically controlled lake-water, each jar containing two specimens. Details of the experimental design are described in Herrmann (1982a). The temperature used in this experiment was gradually adjusted to simulate that of the lake (range $1.5 - 21.0^{\circ}C$). One slightly crushed medium-sized (8 mm) A. aquaticus per D. lacteum was given at weekly intervals. Following the procedure given in Herrmann (1982a), four parameters pertaining to reproduction were determined: 1) number of cocoons deposited, 2) hatching time (in lake temperature sequence as above), 3) number of hatchlings per cocoon, and 4) number of sterile cocoons.

B. Field-produced cocoons (FP). All cocoons deposited underneath 36 concrete bricks in the littoral zone in Lake Bysjön were counted and removed at five day intervals. For description of the concrete brick method, see Herrmann (1979). The treatment of cocoons and parameters obtained were as above.

RESULTS

The number of days required for a cocoon to hatch (D) was found to be inversely proportional to the ambient temperature (T) (Tab. 1). This relation conforms to a power function, on a logarithmic

TABLE 1

Hatching time for incubated cocoons of *D. lacteum* from Lake Bysjön, Sweden (this study) and the Mere, Western Great Britain (Reynoldson et al.1965) at different temperatures. 95 % confidence limits are given.

	Temperature (°C)	Hatching time (days)	Sterility (%)	No.of cocoons
<u>Sweden</u>				
	5	70.2 $\pm$ 2.70	3.4	29
	10	30.8 $\pm$ 1.41	0.0	46
	15	17.4 $\pm$ 0.40	3.1	64
	20	14.6 $\pm$ 0.85	5.6	18
<u>Britain</u>				
	5	73 $\pm$ 4.7	-	23
	10	39 $\pm$ 1.8	-	30
	15	22 $\pm$ 1.3	-	30
	20	19 $\pm$ 1.2	-	38

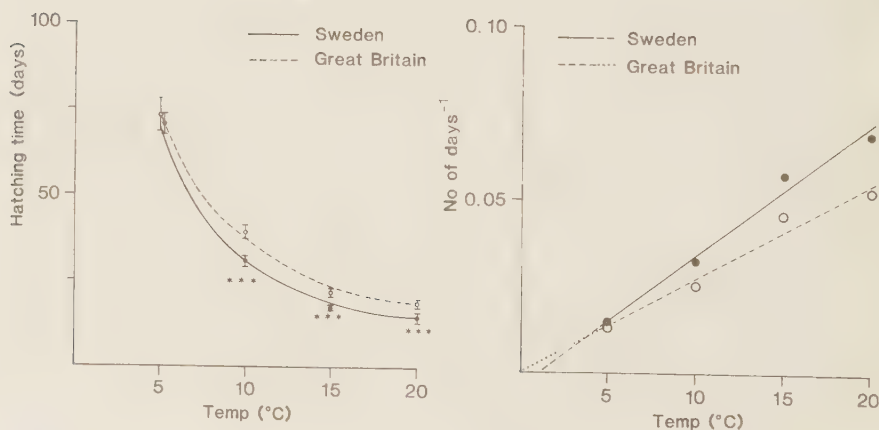


Fig. 1A. Hatching time of cocoons in relation to temperature for cocoons from Lake Bysjön, southern Sweden and The Mere, Western Great Britain. 95 % confidence limits are given.*** denotes a significant difference at the 99.9 % level.

1B. Rate of development in relation to temperature based on the average values from Fig. 1A.

scale described by the equation $\ln D = 6.12 - 1.17 \ln T$; $r = -0.995$, $p < 0.001$ (Fig. 1A).

The number of degree-days required for hatching of cocoons can be calculated by a method adopted from Elliott (1978). Values of the reciprocal of the arithmetic mean of hatching time, here very close to the recommended median value, i.e. the development rate, is plotted against temperature values. If this relationship is linear, the reciprocal of its regression coefficient is the development time and is expressed in units of degree-days above a threshold temperature. The latter is read off where the extrapolated regression line meets the abscissa. Even if this procedure merely results in a theoretical threshold, it allows the calculation of the expected hatching time. Applied to the Swedish data in Tab. 1, the method demonstrates a linear relationship between the two variables ($r = 0.996$) over the temperature range used (Fig. 1B). The number of degree-days required thus was found to be 266 above 1.0°C .

The histological sections of adults showed that the ability of D. lacteum in Lake Bysjön to produce cocoons disappeared in June, as indicated at bottom of Fig. 2A.

The time schedule and properties of cocoons produced in the laboratory and those produced in the field were essentially the same. Thus, the temporal pattern of appearance of cocoons and hatchlings, as well as cocoon sterility showed close agreement in the two situations, although not statistically testable (Tab. 2). Number of hatchlings per cocoon differed slightly between the laboratory- and field-produced cocoons ($p < 0.05$; two-way ANOVA), whereas most variation in the data for hatchlings per cocoon was due to time ($p < 0.001$). Most cocoons were deposited during April and the first half of May, thus forming peak levels in the second half of April (Tab. 2 and Fig. 2B). Number of hatchlings per cocoon in general decreased throughout the spring (Tab. 2). This decline will cause the hatching peak to occur two weeks earlier than would otherwise be the case. Thus the cocoons deposited in the first half of April produced most hatchlings (Tab. 2).

If the time table of cocoon deposition and the calculated number of degree-days and temperature threshold were combined, peak numbers of hatchlings should appear in the second half of May. Because of the number of hatchlings per cocoon is reduced through-

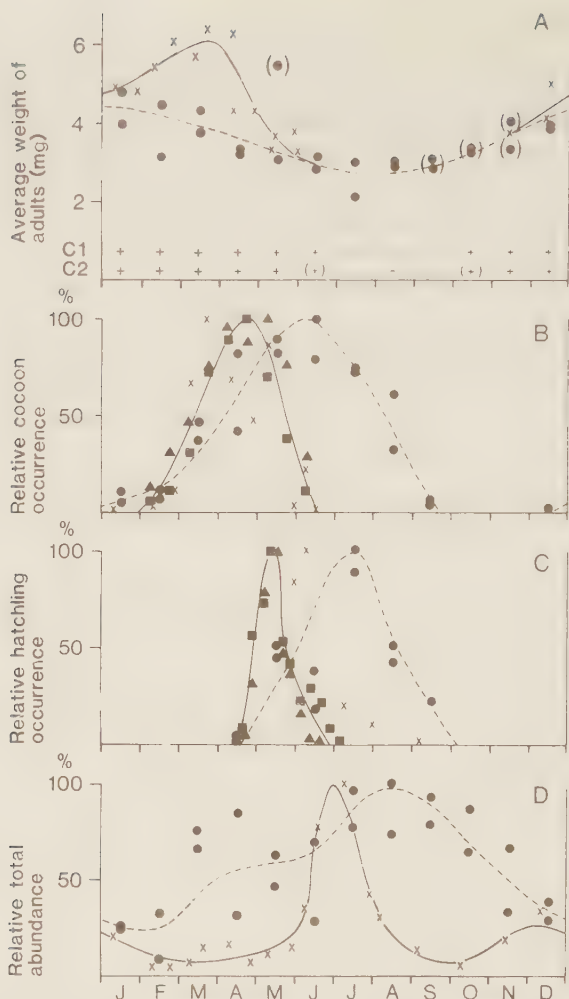


Fig. 2. Comparisons between *D. lacteum* in Lake Bysjön, Sweden (solid line) and Lake Windermere, Great Britain (dashed line), throughout a year. Graphs are fitted by eye.

- A. Monthly average dry weight of adult specimens in the field. Swedish data (crosses) stem from Herrmann (1979). British data (circles) are combined from Wettewé (1974) and Macan and de Silva (1979). At bottom is shown the reproductive state of *D. lacteum* in Lake Bysjön, determined from the criteria c1 = presence of sperm in the spermaducal vesicle, and c2 = presence of ova in the ovary.
- B. Cocoon occurrence, as percent of maximum numbers. Swedish data are "LP-data" in Tab. 2 (triangles), "FP-data" in Tab. ? (squares), and Herrmann (1979) (crosses). British data (circles) are from Wettewé (1974).
- C. Hatchling occurrence, as percent of maximum numbers. Data origin and symbols as in Fig. 2B.
- D. Total abundance, as percent of maximum numbers. Swedish data (crosses) are from Herrmann (1979), British (circles) from Wettewé (1974).

out the spring (see above), this time should be revised to just before the middle of May. This coincides with experimental observations, as depicted in Fig. 2C.

The proportion of sterile cocoons was low for most halfmonth periods, but increased towards the end of the reproductive period (Tab. 2).

TABLE 2

Total number of cocoons, total number of hatchlings from these cocoons, number of hatchlings per cocoon and sterility percentage for half-month periods during the reproduction period of *D. lacteum*. Data sets of two origins are presented; LP = laboratory-produced cocoons (per 20 pairs of *D. lacteum*), FP = field-produced cocoons (per an unknown number). Number of cocoons for which number of hatchlings per cocoon have been estimated equals to the corresponding number of fertile cocoons. 95% confidence limits are given for the number of hatchlings per cocoon.

Period	Number of cocoons		Number of hatchlings from these cocoons		Hatchlings per cocoon (excl. steriles)		Sterility percentage	
	LP	FP	LP	FP	LP	FP	LP	FP
Febr. I	9	6	157	111	17.44 ± 4.83	18.50 ± 7.53	0.0	0.0
Febr. II	21	14	339	243	16.14 ± 2.24	18.69 ± 4.16	0.0	7.1
March I	31	39	494	678	16.47 ± 1.64	17.84 ± 1.88	3.2	2.6
March II	50	90	786	1660	16.04 ± 1.32	18.86 ± 1.42	2.0	2.2
April I	63	108	935	1797	15.08 ± 1.26	17.28 ± 1.12	1.6	3.7
April II	58	121	738	1682	13.18 ± 1.26	14.38 ± 0.85	3.4	3.3
May I	66	85	678	938	10.94 ± 0.89	11.58 ± 0.96	6.1	4.7
May II	51	46	403	440	8.40 ± 1.03	10.23 ± 1.18	5.9	6.5
June I	20	15	113	98	5.95 ± 1.56	7.54 ± 2.91	5.0	13.3
Total:	369	524	4643	7647			3.8	

DISCUSSION

Comparative information on reproductive and related features from different populations often suggests adaptive explanations of differences in physical and biotic regimes. The data presented above will be compared with mainly those from the extensive study of a population of D. lacteum in Lake Windermere, England (Wettewe 1974; Macan and de Silva 1979). Average weight of adults, reproductive status, cocoon deposition, hatchling occurrence and total abundance of D. lacteum were subsequently taken into consideration (Fig. 2). Data from the study of Young and Reynoldson (1966) have also been used.

As none of the British studies mentioned above contained data on cocoon hatching comparable to those obtained here, comparative information from Reynoldson et al. (1965) was used. When their data for a D. lacteum population were analyzed as above, the following temperature-hatching time relationship was obtained: $\ln D = 5.93 - 1.01 \ln T$; $r = -0.993$ (Fig. 1A). At all temperatures except for 5°C, the hatching times of the Swedish population were significantly lower than those of the British one ($p < 0.001$; t-tests). For the British data the number of required degree-days was 366 above -0.1°C.

The peak appearance of cocoons obtained here conforms temporally with other observations in Lake Bysjön (Herrmann 1979 and Fig. 2B), as well as long-term experimental data (Herrmann 1982b). From this, the hatchling peak was expected to occur in the middle of May, as stated above. However, in the field most triclads appeared in the first half of June (Herrmann 1979 and Fig. 2C). The reason for this discrepancy was that, for unknown reasons, the newly hatched triclads avoided the concrete bricks in the lake. This observation is valid also for natural stones (Herrmann 1979). Also, the average size for 144 hatchlings hatched in the laboratory was 2.7 ± 0.4 mm($\pm$ SD), whereas all the 141 hatchlings under the bricks on average were 3.6 ± 0.6 mm($\pm$ SD) ($p < 0.001$; t-test), which clearly indicates that the individuals grow before the re-attachment on the bricks.

As seen in Fig. 2B, the British population showed a much longer period of cocoon deposition; peak densities appeared in early June, but were less prominent. Calculations of the monthly average cocoon output per adult triclad were made. I used comparable data from Wettewe (1974; Fig. 35 and Tab. 40) and Herrmann (1979, Figs 2 and 5), in each case during two breeding seasons.

Also this parameter showed a pronounced difference; 0.29 in Lake Windermere and 0.48 in Lake Bysjön. The values are unfortunately not statistically testable.

According to Wettewe (1974) the most intense hatching was expected to occur about 1 July. This accords with a calculation using temperature data for Lake Windermere (Fig. 3B) and number of degree-days required for hatching. The field data from Lake Windermere, however, showed elevated number of hatchlings in mid July, most probably because of the initial avoidance of bricks, referred to above.

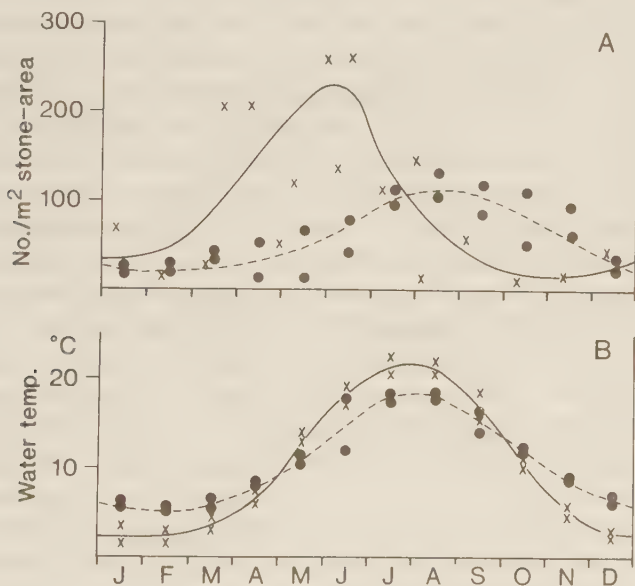


Fig. 3A. Abundance per m² stone-area of *A. aquaticus* in Lake Bysjön (crosses and solid line), and Lake Windermere (circles and dashed line) throughout a year. Graphs are fitted by eye. Data from Herrmann (1979) and Wettewe (1974), respectively.

3B. Monthly average littoral water temperature in Lake Bysjön and Lake Windermere. Symbols, data fitting and origin of data as above.

Thus, both cocoon and hatchling peaks occurred about six weeks later in Lake Windermere than in Lake Bysjön (Figs 2B-C). Curves representing the total abundance of triclads, mainly a function of the recruitment of hatchlings, also showed the same pattern (Fig. 2D).

Young and Reynoldson (1966) report peak abundances of cocoons in the middle of May in Wales. Based on their observations a hatchling peak should be expected in the middle of June, again supported by calculations based on required degree-days. Thus, this population appeared intermediate between those of D. lacteum in Lake Bysjön and Lake Windermere with respect to cocoon deposition and hatching. This was also true for the pattern of total abundance. In accordance with the conclusion above proportionately more hatchlings were observed on leaves than on the bricks also used (Young and Reynoldson 1966).

What causes the Swedish population to begin its reproductive cycle three to six weeks earlier than the British one? The rest of the discussion mainly compares Lake Bysjön to Lake Windermere. Fig. 2A presents the dry weight of an average adult individual of D. lacteum throughout the year in Lake Bysjön and in Lake Windermere. During June-October the Swedish population only consisted of immature ($\leq 3\text{mg}$) individuals (cf. the breeding status in Fig. 2A). The British specimens of adult size ($> 3\text{mg}$) in September-November were probably not functional adults, because during these months they were never found carrying cocoons (Macan and de Silva 1979). The curves depicted in Fig. 2A follow each other during the autumn but diverge considerably during the winter, the greatest difference being reached around the end of March. This period can be expected to be crucial for the main part of the population, by then preparing energetically for the cocoon laying (Fig. 2B).

While the Swedish adults in January-April had the capacity for both growth and reproduction, the British triclads correspondingly showed negative growth, i.e. degeneration and shrinkage. The latter also exhibited comparatively low reproductive output (see above), and at a later stage. The impressive property of D. lacteum to reproduce even in periods of degrowth is well documented by Woollhead and Calow (1979), and is attributed to the resorption of body tissue.

Apart from the significantly shorter hatching times in Sweden (Tab. 1), two other differences should be noted. The number of hatchlings per cocoon, for example, were 14.3 in the present study (average value of the data for Tab. 2), compared to 8.6 (Young and Reynoldson 1966), 9.8 (Macan and de Silva 1979), and 11.5 (Calow and Woollhead 1977). A low proportion of sterile cocoons was also found, viz. 3.8 % (Tab. 2) as compared to 34 %

(Young and Reynoldson 1966), 19 % (Macan and de Silva 1979) and 20-30 % (Calow and Woollhead 1977) in the British populations.

Most of the differences above relate to energy requirements and expenditures. Therefore the most likely causes for the differences observed could be differences in food availability and temperature. A. aquaticus, by far the most important food organism (cf. above), appears earlier and in larger numbers in Lake Bysjön as compared with Lake Windermere (Fig. 3A). An equal utilization of this food in the two lakes could make possible a comparatively larger energy storage before and during the period of cocoon production in the Swedish population compared to the British one. Hence, food alone may account for the observed difference. A plot of values for A. aquaticus from Young and Reynoldson (1966) in Fig. 3A would fall intermediary between that for Lake Bysjön and that for Lake Windermere.

The winter littoral temperature in Lake Windermere was seldom below 5°C and the temperature started to rise somewhat earlier than in Lake Bysjön (Fig. 3B). In the latter the winter temperature often was 1-2°C and the spring rise was much steeper, probably leading to the earlier cocoon and subsequent hatchling peaks. The latter peak was also reinforced by the faster hatching time, higher numbers of hatchlings per cocoon, and lower cocoon sterility in Sweden, all referred to above.

Reynoldson et al. (1965) showed that the hatchlings of D. lacteum cannot mature at 18.5°C or above, and mature most rapidly at a temperature of 10°C. The British lakes seldom exceed 15°C-18°C (Young and Reynoldson 1966; Macan and de Silva 1979). Lake Bysjön shows a temperature regime more of the continental type (Herrmann 1979) and through July and August the average temperature in the littoral was well above 20°C, temporarily exceeding 23°C (Fig. 3B). Such conditions were most probably unfavourable for hatchlings (see also Reynoldson et al. 1965), even if some difference in such a genotypic property can be expected.

Thus, also temperature may contribute significantly to the observed differences. It is suggested that it could be advantageous for the Swedish population to reproduce comparatively early, thus avoiding temperatures lethal for cocoons and hatchlings. In Lake Dojran, Yugoslavia, which showed even higher temperatures in the summer, Sapkarev (1972) found that D. lacteum exhibited a cocoon peak in April and a hatchling peak in May, thus resembling my results. Heitkamp (1979 and pers. comm.) reports a hatchling peak

in mid May for D. lacteum in a pond in southern Germany with summer temperatures $> 20^{\circ}\text{C}$.

D. lacteum live for only one year in Lake Bysjön, followed by a rapid and pronounced deterioration of the adults (Herrmann 1979). This takes place in May-June and coincides with the time when they lose their ability to produce cocoons, indicated by the sectioned specimens (Fig. 2A). This senescence may be responsible for the successive and accentuated decline in numbers of hatchlings per cocoon (Tab. 2).

Thus, it seems reasonable to state that the senescence is dependent on both temperature and food abundance, the latter giving rise to intra-specific competition (see Young and Reynoldson 1966). Boddington and Mettrick (1974) found that a Canadian population of Dugesia polychroa (Schmidt) showed a recruitment with both higher rapidity and larger abundance fluctuations than a comparable British one, and attributed this to a faster temperature rise, and higher food availability, respectively. They then suggested 'that there is less opportunity for competitive feedback from the young to influence the rate of growth, which could in turn result in a higher mortality'. The present comparison seems to be in accordance with this, as the Swedish population, showed a faster and more pronounced recruitment, compared to British ones (Fig. 2D in this paper and Herrmann 1979). It also then seems logical that c. 40 % of the D. lacteum population described by Young and Reynoldson (1966) survived to the next breeding season, while in Lake Bysjön obviously no triclads did so (Herrmann 1979). Further discussions on the longevity of D. lacteum are found in Herrmann (1982b).

As food and temperature seem important for the pattern of reproduction in the different populations, it is legitimate to consider to what extent the observed variations are adaptive. One of the features considered here, namely the relationship between temperature and hatching time, might be expected to reflect a true genotypic adaptation. There are significant differences in this respect between the Swedish and the British populations (Fig. 1). Moreover, these differential temperature responses will considerably add to the success of the two populations, when exposed to the natural temperature regimes. The importance of proper timing of the reproduction in relation to temperature is stressed by Herrmann (1982b).

If, hypothetically, the hatching response of the Windermere population was adopted by the cocoons of Lake Bysjön, the hatching peak would occur about two weeks later, i.e. in the end of June. This would expose the main part of the newly hatched specimens to temperatures of 20-23°C or above, which are probably vulnerable to them (Reynoldson et al. 1965). Thus the differences in the temperature-dependence of the development are of adaptive value in the different habitats.

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PREY CHOICE AND ITS IMPACT ON THE REPRODUCTIVE OUTPUT IN

DENDROCOELUM LACTEUM (TURBELLARIA)

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ABSTRACT

In laboratory experiments the triclad Dendrocoelum lacteum was found to feed predominantly on Asellus aquaticus, but to a minor extent also on amphipods, chironomids, oligochaetes and mayfly nymphs. The actual food choice is suggested to be due to mainly the availability of different food items and the functional ability of the triclad to catch them. Aspects of these requirements and relations to field conditions are discussed. The reproductive output, measured as number of cocoons laid, cocoon size, number of hatchlings per cocoon and the total output of hatchlings increased in most cases when food ration was raised. Maintaining a food niche secures energy for reproduction and some evolutionary aspects on this are discussed. Food availability and consequently intraspecific competition prior to and during the reproductive period is proposed to be a major limiting factor for D. lacteum. Finally, parameters of the reproductive strategy in the present population are compared with data from British investigations and the former are suggested to show r-selected features.

INTRODUCTION

For triclads, sufficient supply of suitable food is crucial not only before reproduction, but is important also throughout the extensive egg-laying period. Triclads are stated to compete intensely for food, both intraspecifically (Reynoldson and Bellamy 1971a) and interspecifically, resulting in partial niche separations (Reynoldson and Davies 1970; Reynoldson and Bellamy 1971b; Reynoldson 1975). Such traits, combined with their expediency in laboratory experiments, make triclads appropriate for qualitative and quantitative analyses of the relationships between food supply and demand.

The most frequent food of Dendrocoelum lacteum (O.F. Müller), at least when occurring together with other triclad species, is isopods of the genus Asellus, but also amphipods and oligochaetes are taken, although less frequently (Reynoldson and Davies 1970; Reynoldson 1975). D. lacteum can actively hunt by gliding on the substrate, reacting on chemical and tactile prey stimuli (Reynoldson and Young 1963; Bellamy and Reynoldson 1974; own unpubl. obs.). Triclads move by means of spreading mucus. This sticky compound promotes the hunting success by entangling the prey in a kind of trap (Reynoldson and Young 1963; de Silva 1976a; own unpubl. obs.), indicating D. lacteum being a "sit and wait" predator (Calow et al. 1981). When a prey contact is established, the triclad quickly folds around the prey. D. lacteum may also use an anterior grasping organ like the confamiliar species Bdellocephala punctata (Pallas) (Adams 1980). The body fluid of the prey is then sucked up through the protrusible pharynx, which also pro-

duces hydrolytic enzymes. For an extensive review of the digestive physiology, see Jennings (1974). As D. lacteum occasionally shows greenish alimentary system, in a preliminary investigation it was provided with green-algae or detritus. Both yielded a reproductive output as low as that of triclads deprived of food (Herrmann unpubl.). This supports the statements of Hyman (1951) and Reynoldson and Young (1963) that D. lacteum is entirely carnivorous. Additional food for the parents is shown to promote the production of offspring in e.g. non-dendrocoelid triclads (Reynoldson 1964) and snails (Eisenberg 1970; van der Steen et al. 1973).

In the present study D. lacteum was confronted with a number of potential prey species, to see whether absence (as in my field locality, see below) of competing triclad species would result in a broader food niche than previously reported. The availability of different prey species in combination with the catching ability of the predator is then supposed to determine the outcome in a choice situation. Further was investigated how the quality and quantity of food influence several reproductive parameters, including production of cocoons and hatchlings, cocoon size and their content of hatchlings.

MATERIAL AND METHODS

Six shore-living lacustrine species are found in South Sweden, but they only rarely occur all together (Herrmann unpubl.). In Lake Bysjön (55°41'N, 13°33'E), described by Herrmann (1979), D. lacteum is by far the dominant triclad species. Asellus aquaticus L. is abundant in the littoral zone, as are gastropods and oligochaetes. These two groups are the main food of Dugesia polychroa (Schmidt) and Polycelis tenuis Ijima, respectively (Reynoldson 1975). Of these two species altogether ca. 5 specimens were collected among thousands of D. lacteum, and they are thus very rare in Lake Bysjön.

In triclads food composition can be studied chiefly in three ways: (1) gut content analyses by squashing whole animals; the method is however not recommended (Reynoldson and Davies 1970), (2) serological analyses of specimens from the field; a reliable but laborious technique, extensively used by Reynoldson and co-workers (e.g. Reynoldson and Davies 1970), and (3) experimental exposure of various prey species to the predator. The latter tech-

nique was chosen for this study, even if objections can be raised also to this method.

All D. lacteum, most prey animals, water and sediment were from Lake Bysjön. Two-litre PVC jars were arranged so that the recirculating, thermostatically controlled lake-water entered through small PVC tubes from above and left through netcovered openings on the side keeping the volume constant at ca. 1.3 l. The average renewal time was ca. 8 min.

CONSUMED AMOUNTS OF DIFFERENT PREY SPECIES (EXP. 1)

Triclads starved for one week were offered different prey items, viz. Oligochaeta spp. (Lumbriculidae and Tubificidae), A. aquaticus, Chironomus plumosus L., Caenis robusta Etn., Gammarus lacustris Sars, Sigara falleni Fieb. and Physa fontinalis L. No other potential prey species occur in Lake Bysjön (Herrmann 1979).

Each set-up with a certain prey species comprised 10 replicates (jars). Three alder leaves per jar gave some shelter for the prey animals. Water temperature was kept constant at 6°C. Remaining prey items were counted daily for 10 days. Then surviving prey items were squashed in the jars and the movement response of the triclads towards the prey item was observed. Jars with prey organisms but without triclads were run as controls. The experiment was conducted in the autumn 1975. Further details are presented in Fig. 1.

Ten to fifty specimens of the different prey items were sampled, dried and weighed. Using information about exoskeleton tissue, ash content and energy content, mainly from Cummins and Wuycheck (1971) and Caspers (1975), the following average energy contents of the body fluid per prey item were estimated: A. aquaticus 88 J, G. lacustris 192 J, Ch. plumosus 38 J, C. robusta 16 J and Oligochaeta spp. 24 J.

PREY CHOICE (EXP. 2)

In a previous experiment (Herrmann unpubl.), D. lacteum was shown to prefer G. lacustris to A. aquaticus, and the latter to oligochaetes, all crushed. However, when live prey items were provided, oligochaetes disappeared most rapidly. In the present experiment these three prey items and also chironomids were used. The condi-

tions in the jars were fairly natural with stagnant water (9°C), leaves, stones and muddy sand from the lake. As the preliminary experiments indicated that G. lacustris also preyed upon oligochaetes, two experimental set-ups were arranged, one with and one without amphipods. Each set-up contained 10 experimental jars and 10 control jars. Apart from this presence or absence of amphipods, the experimental jars contained triclads, starved for one week, A. aquaticus, oligochaetes and chironomids, whereas the control jars contained the same prey items, but no triclads. Number of animals used are found in Fig. 2. The number of surviving prey items were recorded after 2, 4, 8 and 10 days. The experiment was conducted in the autumn 1975.

REPRODUCTIVE OUTPUT (EXPS 3 AND 4)

The impact of type and quantity of prey items on the reproductive output of D. lacteum was investigated (Exp. 3). Five identical jars, devoid of substrate, were run with each food regime. Each jar contained two D. lacteum and either no food, A. aquaticus, G. lacustris, Ch. plumosus, C. robusta or Oligochaeta spp. in numbers outlined in Tab. 1. Prey items were slightly crushed to ensure consumption by D. lacteum, as the aim was to register consequences of different diets *per se*, not the catching ability. Mostly only exoskeleton fragments remained after the meals. In order to include possible effects of food differences on the development of the reproductive organs the experiments started ca. 1 December. The water temperature during the experiments and the following incubations closely followed that of the lake. The experiment was performed during winter-spring 1976.

Four different aspects of the reproduction were estimated: (1) Cocoons were counted daily and removed from the jars. (2) Cocoon diameters were measured using a binocular microscope with micrometer eye-piece. Incubated individually in glass test-tubes, the cocoons were inspected daily to register (3) hatching time and (4) number of emerged hatchlings.

The reproductive output of D. lacteum when 1 or 2 A. aquaticus (ca. 8 mm) per D. lacteum and week were offered as food were further treated in an extended study. Each food regime was presented to 2 D. lacteum in 12 jars without substrate (Exp. 4). The temperature regime and estimation of reproductive output were as in Exp. 3. The experiment was performed during spring 1977.

RESULTS

When offered the seven different prey items, one at a time, D. lacteum did not feed on P. fontinalis and S. falleni (Fig. 1). Therefore, and as they evoked only weak responses as crushed, these two prey items were regarded as being of no substantial importance to D. lacteum and discarded in the further experiments. The other prey items were all consumed, although at different rates. All the oligochaetes were devoured after 6 d, while of the other prey species some survived until the end of the 10 d long experiment. The variation in consumption within the whole experimental set-up were after both 6 and 10 d significant ($p < 0.001$; Kruskal-Wallis one-way analysis of variance) (Fig. 1). Oligochaetes were significantly ($p < 0.05$ or less) faster consumed than any other prey item. Considering the amount of energy consumed, D. lacteum ingested, on average, most energy when A. aquaticus was provided ($p < 0.05$ or less after 6 and 10 days, Kruskal-Wallis) and least when C. robusta was the prey. In the control jars the natural mortality of prey items was virtually zero (A. aquaticus) or zero (the others).

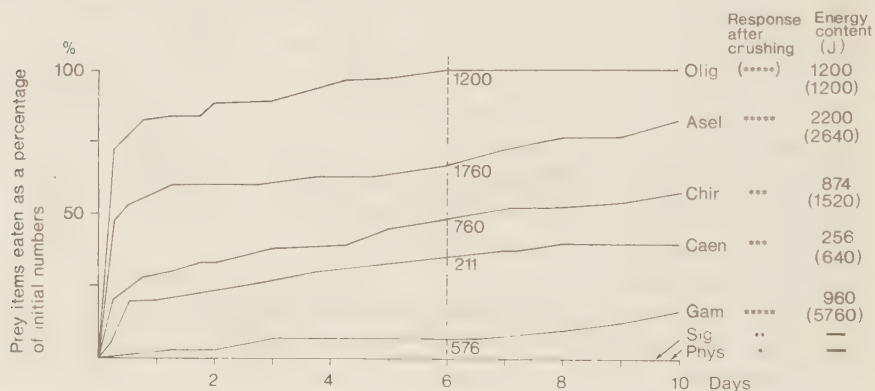


Fig. 1. Consumption of different prey species, one at a time, by Dendrocoelum lacteum. For each prey species 10 jars were used, each with 5 tri-clads. The prey species used and numbers per jar were: Olig = Oligochaeta spp.(5), Asel = Asellus aquaticus(3), Chir = Chironomus plumosus(4), Caen = Caenis robusta(4), Gam = Gammarus lacustris(3), Sig = Sigara falleni(3), Phys = Physa fontinalis(3). Responses on crushed prey items indicated semiquantitatively, where * means very weak and ***** very strong. Energy amounts consumed after 6 and 10 days are given, and within brackets, the energy of the total offered food rations.

Crushed A. aquaticus, G. lacustris and oligochaetes caused a very marked response of the predator in Exp. 1. These species and chironomids were used in the choice experiments (Exp. 2; Fig. 2). Important to note is that all consumption graphs in this figure are results after subtraction of prey item losses in the control jars. Irrespective of presence of G. lacustris or not, A. aquaticus was consumed to a much higher degree than all the others ($p < 0.05$ or less, Kruskal-Wallis).

The importance of food quality and quantity for the reproductive output was analysed in Exp. 3, where all the species consumed by D. lacteum in Exp. 1 were used as prey (Tab. 1). All significance tests on values in Tab. 1 are two-way ANOVA. In the rest of this paragraph, figures within brackets indicate numbers per D. lacteum and week. Three food regimes supported a significantly higher production of cocoons and hatchlings than the other regimes ($p < 0.001$). These were A. aquaticus (2), A. aquaticus (1), and Ch. plumosus (2), of which the first regime produced significantly more hatchlings than the other two. Five regimes, i.e. A. aquaticus (0.5), G. lacustris (0.25), G. lacustris (1), Ch. plumosus (0.5), and Oligochaeta spp. (8), resulted in only small numbers of cocoons. Three regimes, namely Oligochaeta spp. (1.5), C. robusta (2), and C. robusta (10), caused total failure of cocoon production, as did the reference regime with total starvation.

The impact of the available quantity of the most preferred food on the production of cocoons and hatchlings was further tested in Exp. 4. Significant differences ($p < 0.05$ or less; indep. t-test) were found between the two food regimes for most parameters over the whole reproductive period (Tab. 2). When analysed on a half-month time basis (Fig. 3), all reproductive parameters were significantly different in the two food regimes ($p < 0.01$ or less), but showed also a significant change with time throughout the spring ($p < 0.001$, both tests were two-way ANOVA). Here it should be pointed out, that the number of hatchlings indicated for a certain half month in Fig. 3B did actually hatch later, but originated from cocoons produced during this certain period (Fig. 3A).

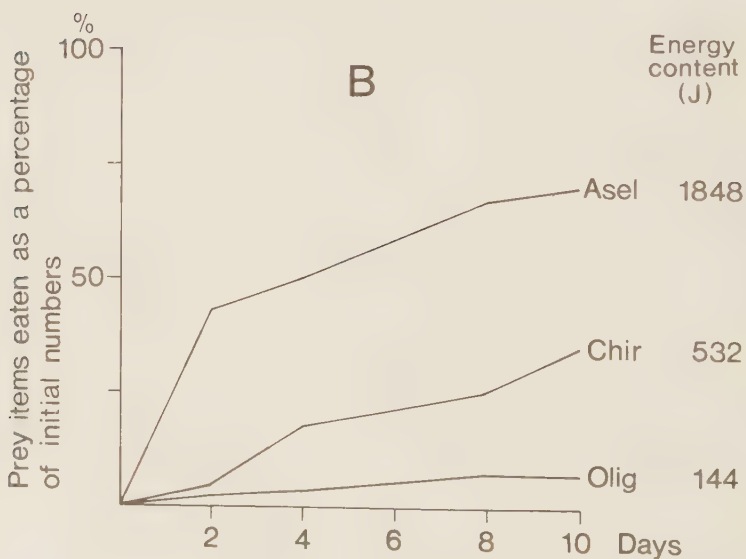
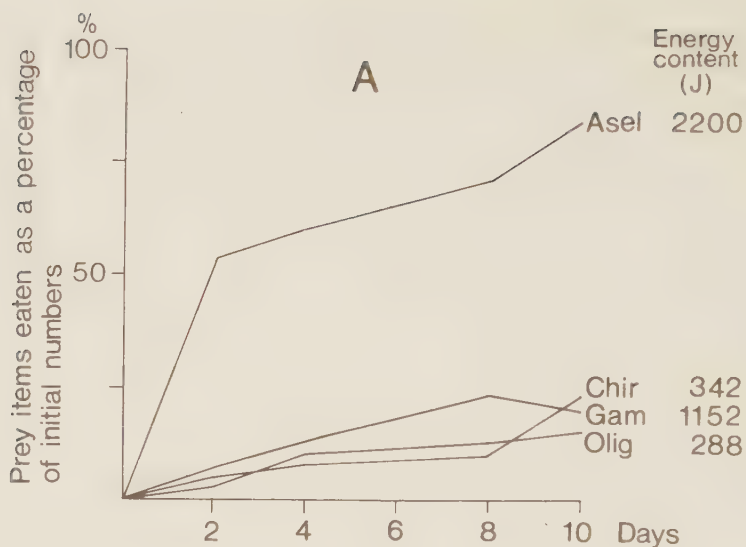


Fig. 2. Food choice of *D. lacteum* between living prey items on natural substrate. The graphs show its real consumption, i.e. after prey item losses in the control jars were subtracted.
 A. Ten jars, each with 3 *D. lacteum* + 3 *A. aquaticus* (Asel), 3 *G. lacustris* (Gam), 8 *Oligochaeta* (Olig) and 4 *Chironomus plumosus* (Chir). Besides 10 jars as above but without triclad were run as controls.
 B. As in A, but without *G. lacustris*.

TABLE 1

Reproductive output for *D. lacteum* under different food regimes, given as cocoon production per 2 weeks, and for the whole season, production of cocoons and hatchlings, cocoon size and their content of hatchlings (the latter two with 95 % confidence limits). Each row comprises 5 jars, each with 2 *D. lacteum*. Weekly addition of prey items and the energy content of this ration are indicated. Asellus = *A. aquaticus*, Gammarus = *G. lacustris*, Chiron. = *Ch. plumosus*, Oligoch. = *Oligochaeta* spp., Caenis = *C. robusta*. All values are based on 10 *D. lacteum* or the summarized cocoons from these, whereas statistics presented in the text are performed on the five replicates, each with 2 *D. lacteum*.

Feeding regime	Asellus ₁ .5week ₁	Asellus ₁ 1 week	Asellus ₁ 2 week	Gammarus ₁ .25week ₁	Gammarus ₁ 1 week ₁	Chiron ₁ .5week ₁	Chiron ₁ 2week ₁	Oligoch. 1.5week ₁	Oligoch. 8week ₁	Caenis 2week ₁	Caenis 10 week ₁	No food
Energy content (J)	44	88	176	48	192	19	76	36	192	32	160	-
December I												
December II												
January I												
January II	2	1										
February I	2	3			1							
February II	3	4			4							
March I	4	8					1		1			
March II	9	10			3		3					
April I	1	10	15	5	3	4	5					
April II	1	10	16	3	2	6	14		1			
May I	4	6				4	17		1			
May II	4	6				4	10					
Σ cocoons	2	44	63	8	13	19	50	-	3	-	-	-
Average cocoon size (mm)	1.9	2.1±0.1	2.3±0.05	2.5±0.2	2.5±0.2	2.1±0.2	2.0±0.1		2.0			
Average number hatchlings per cocoon (excl. steriles)	7.0	13.2±1.4	13.5±1.6	17.0±4.7	17.8±4.7	10.1±2.4	10.8±0.9		15.0			
Σ hatchlings	7	554	1089	136	214	182	531		45			
Percentage ster- ile cocoons	50	4.5	6.4	0	7.7	5.3	2.0		0			

TABLE 2

Overall season characteristics of cocoon-laying and cocoons from two groups of D. lacteum, fed on two rations: 1 and 2 A. aquaticus per D. lacteum weekly, respectively. 95% confidence limits are given, n values within brackets.

	1 <u>A. aquaticus</u>	2 <u>A. aquaticus</u>
Average size of cocoons (mm)	2.1 ± 0.04 (148) (p<0.001)	2.3 ± 0.03 (233)
Average number of hatchlings per cocoon (steriles excluded)	14.4 ± 1.2 (140) (p<0.05)	16.2 ± 0.9 (223)
Total number of cocoons per 2 <u>D. lacteum</u>	12.3 ± 2.87 (12) (p<0.001)	19.4 ± 2.69 (12)
Total number of hatchlings per 2 <u>D. lacteum</u>	169 ± 33.5 (12) (p<0.001)	312 ± 55.3 (12)
Percentage sterile cocoons	5.8 ± 6.0 (12) (p>0.1)	4.3 ± 6.9 (12)

DISCUSSION

The main prey component in a predator's total food niche was by Reynoldson (1966) aptly named "the food refuge", which in itself does not imply any real choice or preference. This concept was later defined as that part of the diet on which a particular triclade species is competitively superior (Reynoldson 1975), enabling co-existence with competing species, shown for triclads in laboratory experiments (Reynoldson and Bellamy 1973). The more narrow and species-specific this food refuge is, the less will overlap and competition with other predators become.

The amount of food taken outside the food refuge depends mainly on the competitive pressure from other predators demanding for the same resources. Consequently, the abundance of a particular food refuge (prey species) will influence the reproductive success of the predator. Further, when competing species are constantly absent the predator may expand its food niche and take a greater

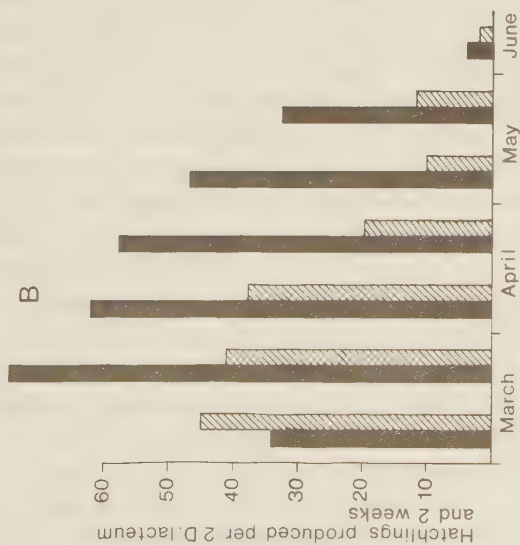
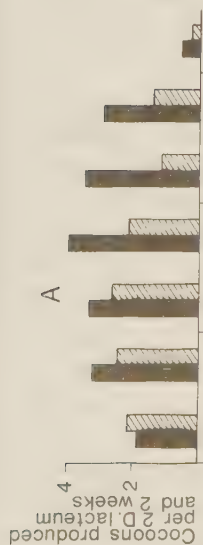
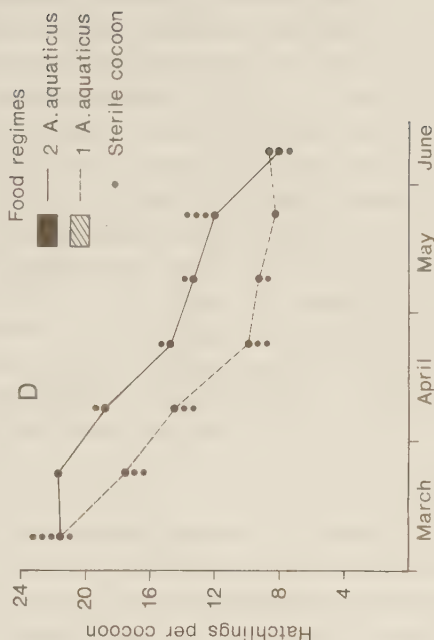


Fig. 3. (A) Average number of cocoons produced, (B) average number of hatchlings (originating from the same period), (C) cocoon size, and (D) hatchlings per cocoon (steriles excluded) during the reproduction of *D. lacteum* with the food regimes 1 and 2 *A. aquaticus* per *D. lacteum* weekly. For bar values, $n = 12$. For graph values, n is equal to the number of cocoons for respective group and period multiplied by 12.



variety of suitable prey species. Such an ecological release with respect to food implies the prerequisite of a potential functional ability of the triclad to catch an alternative prey item, i.e. the absence of a definitive and total genetic fixation of the prey catching behaviour. Thus Reynoldson and Davies (1970) reported that Polycelis nigra (O.F. Müller), normally eating oligochaetes and virtually no A. aquaticus, took much more isopods in some Welsh lakes where D. lacteum was absent. Similarly, P. tenuis has been shown to eat significantly more snails in lakes where Dug. polychroa was absent (Reynoldson and Pearce 1979a).

In British studies on feeding in triclad (e.g. Reynoldson and Young 1963; Reynoldson and Davies 1970; Reynoldson 1975; de Silva 1976b), D. lacteum always co-occurred with other triclad. The virtual absence of other triclad competitors in Lake Bysjön might be expected to allow an expanded range of food items in the diet of D. lacteum.

The reason for the inability of D. lacteum to take P. fontinalis (Fig. 1) can partly be that also gastropods use a mucus layer (cf. however Reynoldson and Pearce 1979b). That no consumption of the temporarily abundant S. falleni occurred may be due to the fact that it mostly moves off the bottom, moves too fast and is less easily penetrated by the triclad pharynx. When crushed these two items did only weakly attract the triclad, and are concluded to have no importance as food for D. lacteum, in accordance with Reynoldson and Young (1963) and Reynoldson (1975). On the basis of the low capture success (35 and 40 % after 6 and 10 d, respectively) and weak response for C. robusta (Fig. 1), this species is regarded of little importance as food for D. lacteum. The amphipod G. lacustris provides a potentially large food resource, in terms of its size, but is rather difficult to catch for the triclad due to its fast movements. Consequently, only 7 and 17 % of the offered individuals were captured within 6 and 10 d, respectively.

Oligochaetes were most rapidly consumed in Exp. 1 (100 % after 6 d), closely followed by A. aquaticus (67 and 83 % eaten after 6 and 10 d, respectively; Fig. 1) and at a lower rate Ch. plumosus (50 and 58 %, respectively). In terms of energy the importance of oligochaetes and chironomids seems less than A. aquaticus (Fig. 1). In the choice situation in Exp. 2, D. lacteum, however, captured mainly A. aquaticus, for certain because a natural substrate was used, which facilitated the burrowing and tube-making of oli-

gochaetes and chironomids (Fig. 2). Based on this it seems legitimate to regard chironomids and oligochaetes of minor importance as food for D. lacteum. That these prey items lack external appendages has been claimed to be disadvantageous for the hunting success of B. punctata (Adams 1980).

De Silva (1976b) also found that D. lacteum readily devoured oligochaetes and chironomids when no substrate was present, but not under natural conditions. Pickavance (1968; in Reynoldson and Davies 1970) used serology to test whether D. lacteum consumed chironomids, but none was recorded.

Interestingly, some of the prey items consumed in Fig. 2A were most certainly captured by G. lacustris. When this predation pressure was eliminated, A. aquaticus and oligochaetes survived better (Fig. 2B). At the same time (non-significantly) higher numbers of chironomids were preyed upon, most certainly by D. lacteum. Thus, it seems as if G. lacustris could suppress the ability of D. lacteum to take chironomids. Hence the importance of these might be larger than outlined above.

The results in Exps 1 and 2 suggest that A. aquaticus is the main prey item for D. lacteum, thus confirming British findings (e.g. Reynoldson and Davies 1970; de Silva 1976b). Also the triclade B. punctata seems to utilize this food refuge, but preferably the larger specimens (Adams 1981). In Sweden it is almost exclusively confined to eutrophic lakes (Dahm 1956, Herrmann unpubl.). That A. aquaticus is important for D. lacteum is further indicated by an analysis of the occurrence of both species in 115 lakes in South Sweden (Herrmann 1982a).

The triclads reared on amphipods, mayflies and oligochaetes in Exp. 3 exhibited low fitness in the sense that they produced small or no quantities of hatchlings (Tab. 1). These prey items would then be expected to be of less importance to D. lacteum in a natural population.

Supposing that the outcome in a natural choice situation is actually ruled by the ability of a predator to take the different prey items and the availability of these, the substrate in Exp. 2 would fit the prey items properly and offer D. lacteum a fairly natural choice situation. That D. lacteum can choose proper chemical and tactile stimuli from A. aquaticus was shown by Bellamy and Reynoldson (1974). Counted in percentage on an energy basis, the importance of each prey item as part of total consumption after 10 days in Fig. 2A was calculated. This yielded the figures

A. aquaticus 55 %, G. lacustris 29 %, chironomids 9 % and oligochaetes 7 %.

A British D. lacteum population was serologically shown to eat Asellus, Gammarus and Oligochaeta in the proportions 64, 23 and 13 %, respectively (Reynoldson 1975). Chironomids were not included. The present study suggests that, in the absence of amphipods, chironomids can constitute as much as 21 % of the diet of D. lacteum (energy figures in Fig. 2B). Thus, the role of chironomids might be underestimated by Reynoldson. A tentative correction for this can be made by taking 9 % (= the chironomid part, see above) of Reynoldson's data for the other items and lump into a new group. Then, the British figures become: 58, 21, 9 and 12 % of Asellus, Gammarus, oligochaetes, and chironomids, respectively. In a Scottish lake chironomids formed 9 % of the food of D. lacteum, also in the absence of amphipods (serological tests; Reynoldson and Sefton (1976)).

Thus, in general, the food choice of D. lacteum in the present experiments seems rather consistent with field conditions in Britain. This could be interpreted as if the D. lacteum population in Lake Bysjön, not being confronted with any triclad competitors, constitute its food composition in the same proportions as did the British one, where D. lacteum existed together with other triclads. If so, this would be a situation where an ecological release with respect to food is possible but not realized. One reason for this could be that genetical constraints have evolved in D. lacteum in general. Through natural selection, the result becomes a genetical conservation of morphological and behavioural attributes that yield the most favourable prey item(s), including aspects as prey abundance, catchability, handling time, and nutritional value.

However, the realized feeding niche in the field is probably mainly a function of the availability of different food items and the ability to take them, aspects that are much depending upon the microhabitat structure but also existing competitors. Obviously, in Lake Bysjön G. lacustris is a potential competitor to D. lacteum, others might be leeches (see Young and Ironmonger 1980). For these reasons one is inclined to agree with Adams' (1980) statement that a laboratory food choice result is only precompetitive, thus representing the fundamental food niche.

Summarizing the experiments with different prey items, it is suggested that A. aquaticus is the main food item, but that amphi-

pod and chironomid are also of some importance. It should be noted that Reynoldson (1975) points out that 'the operation of food refuges is a combination of innate preference and opportunistic behaviour involving competition'.

Comparisons with a study of the field reproduction phenology in D. lacteum in South Sweden (Herrmann 1982b) implies that an adequate normal consumption rate is slightly more than 1 A. aquaticus per D. lacteum weekly. This conforms with a figure of 1.4 yielded from calculations made from Fig. 10 in Wettewé (1974).

By doubling the number of A. aquaticus offered as food from 1 to 2 per D. lacteum and week, the cocoon production increased significantly, and so did the number of hatchlings per cocoon (Tab. 2, Fig. 3A-B). For the regimes in Tabs 1 and 2 which produced more than 10 cocoons during the whole reproduction period, the number of hatchlings per cocoon over the whole period was closely related to the energy content per meal ($r = 0.940$, $p < 0.001$, $n = 7$). As thus the reproductive output is significantly related to consumed energy, food availability probably is of considerable importance to D. lacteum not only before but also during the reproduction period. Therefore, intraspecific competition will considerably affect the reproductive success and is regarded as an important limiting factor.

Calow and Woolhead (1977), in a study similar to this, found that increased food quantity promoted cocoon production, although much less pronounced effects were obtained. The same authors reported that, irrespective of food consumption, the number of hatchlings per cocoon appeared about the same; grand mean 11.5. The present experiments mostly gave higher figures (range 8 - 22; Fig. 3D). The former study showed 20-30 % sterile cocoons, compared to ca. 5 % sterility in the present investigation. The food regimes 1 and 2 A. aquaticus per D. lacteum weekly (Tab. 2) yielded 63 and 147 hatchlings per adult per 10 weeks, respectively. Comparable data in Calow and Woolhead (1977) seemed to be 76 and 86 hatchlings, respectively. Obviously, the Swedish population, with respect to reproduction seems to have a stronger response to increased food availability. In an earlier paper (Herrmann 1979) I proposed the D. lacteum population in Lake Bysjön to have adopted more of an r-strategy than have British populations. This seems justified also with regard to the present data.

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TEMPERATURE-DEPENDENCE OF REPRODUCTION IN DENDROCOELUM LACTEUM
(TURBELLARIA) - AN EXPERIMENTAL APPROACH

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In laboratory experiments with the triclad Dendrocoelum lacteum (O.F. Müller) cocoon deposition was found to occur between 2°C and 20°C with an optimum temperature at 10°C. Temporally displaced spring temperatures could either accelerate or retard the reproductive performance, respectively. A proper timing of the reproductive cycle is maintained by means of temperature conditions, thereby assuring the cocoons and hatchlings the most favourable temperature conditions. The reproductive pattern is suggested to depend on a combination of temperature, food conditions and age of the adults. Animals starved at 15°C shrank more and produced more cocoons than at 5°C, thereby more seriously impairing the former. When fed again, both regimes recovered in 1-2 months. The 5°-animals survived for three years, displaying an intrinsic seasonal reproductive pattern. That D. lacteum, at least in Sweden, is totally semelparous is suggested to be due to food and temperature conditions, causing a high degree of energy allocation on reproduction, and thereby recklessness and lowered life expectancy of the adults.

1. INTRODUCTION

In poikilothermic invertebrates the phenology and fecundity are often considerably affected by temperature. This has been especially emphasized for insects, e.g. Ward and Stanford (1982). Reynoldson et al. (1965) estimated the effect of constant temperatures on different stages (e.g. cocoon production, cocoon development and maturation) of the life cycles in four species of lake-dwelling triclads and also presented upper and lower temperature limits for these different stages.

However, for species with a long reproductive period the relationship between fecundity and temperature is particularly important. In the present study this has been investigated in Dendrocoelum lacteum (O.F. Müller), a common annual and semelparous triclad. Previously its population dynamics in South Sweden and its reproductive output in a natural temperature sequence were investigated and compared with British populations by Herrmann (1979 and 1982a, respectively).

Based on these previous investigations the following hypotheses will be tested: 1/. That an early spring rise in temperature causes an earlier cocoon deposition and earlier appearance of hatchlings. 2/. That a delayed spring, similarly, results in later cocoon and hatchling performances. 3/. That the total output of cocoons and hatchlings per season will on average be greatest at a natural temperature sequence, i.e. the field temperature is optimal in terms of reproductive output.

Even at food shortage, triclads can, by means of degrowth and resorption of their body tissue, continue to reproduce, although

at a reduced level (Woolthead and Calow 1979). The extent to which this catabolic process, measured as reproductive output, is temperature-dependent, will also be described. Finally, the extent to which triclads under constant temperature, food and light conditions (complete darkness) can conserve their basic seasonal reproductive periodicity will be considered.

2. MATERIAL AND METHODS

Specimens of D. lacteum were from Lake Bysjön (55°41'N, 13°33'E), described in detail by Herrmann (1979). Jars supplied with recirculating, thermostatically controlled lake-water were used, each containing two triclads, for details see Herrmann (1982b). Food ration was, unless otherwise stated, one slightly crushed Asellus aquaticus L. (c. 8 mm) per triclad and week. In accordance with the procedure given by Herrmann (1982b), the following parameters were recorded: (1) Number of cocoons deposited, (2) number of sterile cocoons and (3) number of hatchlings per cocoon. All cocoon incubations below were carried out in 20°C.

2.1. TEMPERATURE-REGIME MANIPULATIONS

Five groups, each with 15 jars, were set up in the end of February 1978, when the lake water temperature was about 1°C. Thereafter each group was subjected to a specific and controlled temperature regime, viz.:

Exp. A. Temperature closely followed lake conditions. It was gradually increased from 1.5°C to 20°C between 1 March and 15 June, and then kept constant at 20°C until 1 August.

Exp. B. Temperature elevation was about half that of Exp. A. 1.5°C on 1 March was gradually increased to 14°C on 1 August.

Exp. C. 1.5°C on 1 March was gradually increased at almost twice the rate of Exp. A to 20°C on 8 May. Beginning on 15 May, temperature was successively lowered during one week to 10°C, where it was kept until 1 August.

Exp. D. Started as Exp. C, but when 10°C was reached on 7 April, the system was brought back to winter conditions, 1.0°C, kept so until 15 June. Then during one week temperature was continuously raised to 10°C, kept so until 1 August.

Exp. E. 1.5°C on 1 March was gradually increased, at about six

times the rate of Exp. A, to 10°C on 8 March, kept so until 1 August.

2.2. STARVATION AT DIFFERENT TEMPERATURES

Starting at the end of January 1977, two groups of 13 jars, each with two triclads, were supplied with water respectively at 5°C and 15°C. The two groups of animals were initially very similar in size composition ($\text{mm} = 16.23 \pm 2.79$ (SD) and 16.30 ± 2.76 , respectively). All triclads were first starved for two months. Failure of a cooling bath killed the 15°C-animals at the end of March, while the 5°C-animals were kept for altogether 2.5 years. From 24 March they were fed again (standard ration, see above) to determine how rapidly they could recover from their impaired condition and for how long time altogether they could reproduce. In order to assess any intrinsic rhythmic pattern of the reproduction, the jars were at this time transferred to complete darkness. The length of the specimens was measured fortnightly during the first 16 months (for technique see Herrmann 1979). The number of cocoons deposited was noted throughout the experiment, whereas the number of hatchlings per cocoon was estimated during the first six months.

3. RESULTS

3.1. DO TEMPORALLY DISPLACED SPRING TEMPERATURES ALTER THE COCOON DEPOSITION EVENTS?

As compared with the natural situation (Exp. A), the delayed spring temperature in Exp. B caused a delayed cocoon deposition, and the earlier spring temperatures in Exp. C caused an earlier cocoon deposition (Fig. 1). Evidently, temperature is of great importance for the time schedule of cocoon deposition in D. lac-teum. Both comparisons showed significant differences ($p < 0.001$, d-test for large normally distributed samples, using number of weeks as variable, Bailey 1959 p. 35).

3.2. IS THERE AN OPTIMAL TEMPERATURE FOR THE COCOON DEPOSITION?

Maximum output of cocoons on average was at about 10°C, one exception being Exp. C (Fig. 1C). In this case a high cocoon out-

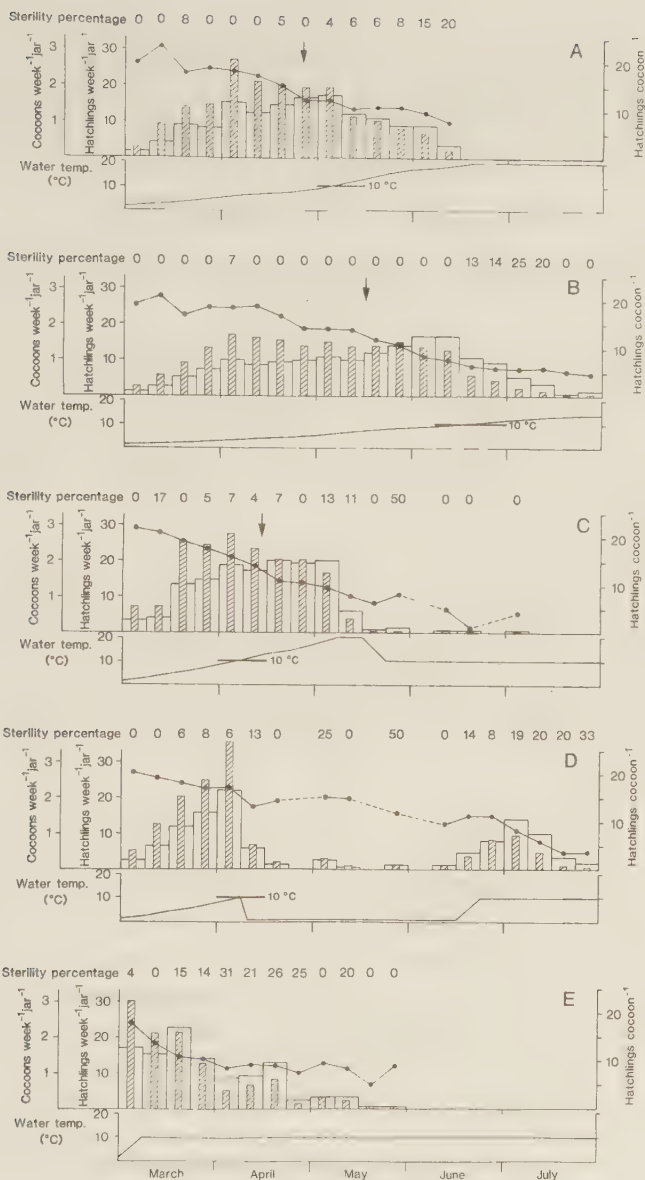


Fig. 1. Weekly cocoon production (open bars), hatchling production originating from the same period (hatched bars), number of hatchlings per cocoon (filled circles), and percentage cocoon sterility for *D. lacteum* under different temperature regimes (drawn at bottom of each figure). In A-C arrows indicate the mean time for cocoon production. Each regime comprised 15 jars with 2 *D. lacteum* in each, all fed with 1 *A. aquaticus* per triclud and week.

put continued up to 18-19°C, thereby coinciding in time with the peak deposition in the field. Using time as variable and cocoon output as frequency function of this as in 3.1, the mean occurred at a temperature of around 8°C in Exps A and B, but at 12°C in Exp. C.

3.3. ARE THERE LOWER AND UPPER TEMPERATURE LIMITS FOR THE COCOON DEPOSITION?

The ability of D. lacteum to produce cocoons at 1°C seemed limited (Fig. 1D). A subsequent pronounced temperature rise induced a renewed cocoon deposition, in spite of the unnatural season. Maximum temperature for cocoon laying was around 20°C (Figs 1A and 1C). Also the number of reproducing triclads decreased at this temperature.

3.4. DOES THE NUMBER OF HATCHLINGS PER COCOON VARY WITH TIME?

Here it should be pointed out that the number of hatchlings indicated for a certain half month in Fig. 1 did actually hatch later, but originated from cocoons produced during this certain period. Thus a certain hatchling bar refers to the cocoon bar for the same week.

This taken into account, it will be found that peak levels of hatchlings generally appeared 2-3 weeks before the period when most cocoons were deposited. This indicates a subsequent decrease in the number of hatchlings per cocoon and/or increased sterility. Both were found to occur in all experiments (Fig. 1A-E, see also Herrmann 1982a). The return to winter temperatures in Exp. D seemed to give rise to the number of hatchlings per cocoon were maintained at a relatively high level for a longer period.

3.5. IS THE TOTAL OUTPUT OF OFFSPRING HIGHEST AT A NORMAL TEMPERATURE REGIME?

All statistical tests in part 3.5 were one-way ANOVA. Tab. 1 summarizes the reproductive parameters obtained from the five experiments. Total cocoon output was higher in Exp. B ($p > 0.05$), while the lowest figures were obtained at the most unnatural temperature conditions (Exps D-E; $p < 0.05$), and Exps A and C resul-

TABLE 1

Number of cocoons, number of hatchlings, average number of hatchlings per cocoon, and sterility percentage for the whole reproductive season of D. lacteum under the temperature regimes depicted in Fig. 1. 95 % confidence limits are indicated, n = 15 in all cases.

Experiment	Number of cocoons jar ⁻¹	Number of hatchlings jar ⁻¹	Hatchlings per cocoon (excl. steriles)	Sterility percentage
A	14.2 ± 1.5	186 ± 18.3	13.8 ± 0.9	4.0 ± 2.6
B	16.6 ± 1.8	193 ± 23.5	12.1 ± 0.8	3.1 ± 2.8
C	14.0 ± 2.0	178 ± 30.8	13.4 ± 1.1	5.2 ± 3.2
D	11.3 ± 2.6	141 ± 23.2	15.1 ± 1.9	11.4 ± 4.5
E	10.9 ± 2.4	113 ± 26.2	12.3 ± 0.8	14.7 ± 8.1

ted in intermediate values. The same pattern recurred when total number of hatchlings was compared. In this respect, the difference between Exps A, B or C versus D or E were highly significant ($p < 0.01$ or less). The average numbers of hatchlings per cocoon were essentially the same in the different experiments, although lower in Exps B and E ($p < 0.05$ or less). Sterility was quite low in Exps A-C, but considerably higher in Exps D-E ($p < 0.05$ or less).

3.6. HOW DOES COMPLETE STARVATION AFFECT THE OFFSPRING OUTPUT, DEPENDING ON TEMPERATURE?

All statistical tests in part 3.6 were two-way ANOVA. D. lacteum responded differently at 5°C and 15°C (Fig. 2). In both situations the triclads shrank significantly with time ($p < 0.01$), but much more so at 15°C than at 5°C ($p < 0.001$). The number of produced cocoons and hatchlings decreased significantly with time ($p < 0.001$ and $p < 0.01$, respectively). Notably higher outputs of cocoons and hatchlings were yielded at 15°C than at 5°C during the first half starvation period ($p < 0.01$ and $p < 0.05$, respectively). During the second half the difference between the two temperatures was reversed, but was not significant. The number of hatchlings per cocoon decreased in both groups with time ($p < 0.05$), but this was much more pronounced at 15°C than at 5°C ($p < 0.05$). The proportion of sterile cocoons was low in both situations.

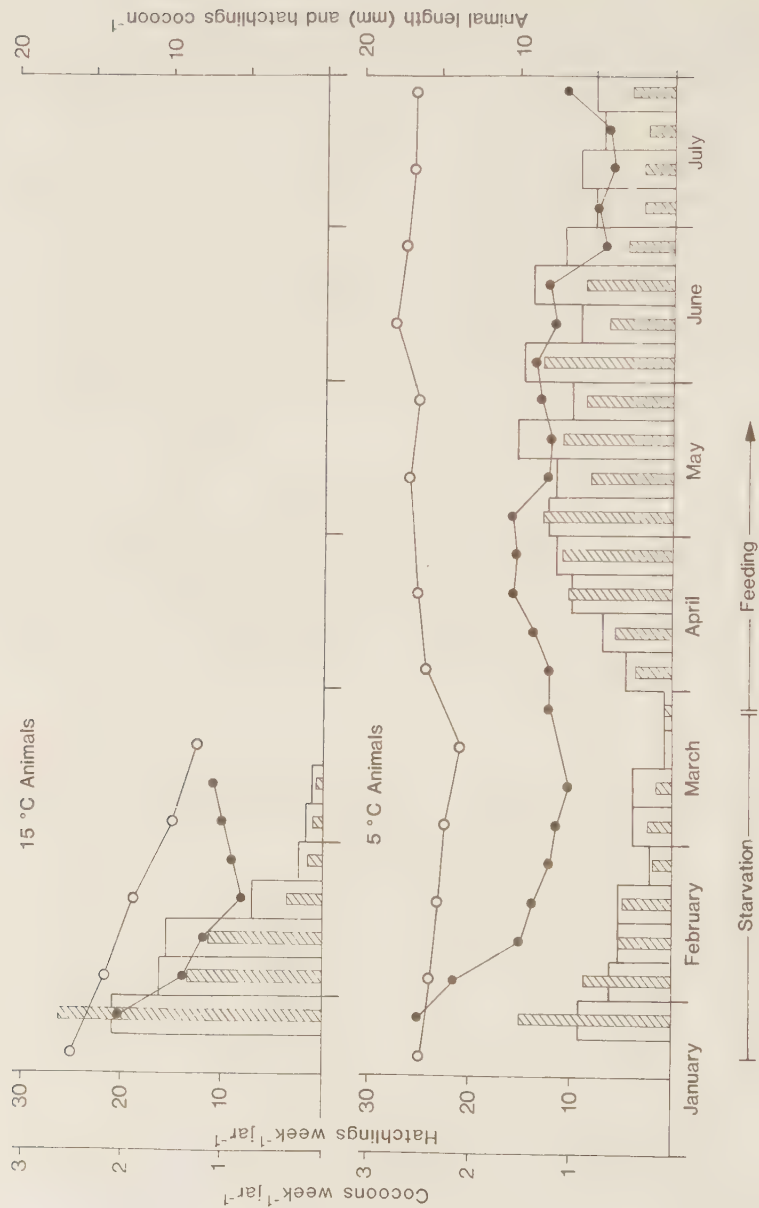


Fig. 2. Animal length (open circles), weekly cocoon production (open bars), hatchling production originating from the same period (hatched bars), and number of hatchlings per cocoon (filled circles) for *D. lacteum* at constant temperatures; 5°C and 15°C. Each regime comprised initially 13 jars with 2 *D. lacteum* in each. Feeding, when it occurred, was 1 *A. aquaticus* per tritlad and week.

3.7. CAN TRICLADS SUPPRESSED BY A PERIOD OF STARVATION RECOVER IN REPRODUCTION?

The 5°C-animals regained their initial size in a few weeks as a result of recommended feeding at the end of March (Fig. 2). The average size of the triclads thereafter remained around 17 mm. Weekly cocoon production also rose and became even larger than the initial values ($p < 0.01$; sign test, Siegel 1956 p. 68). As the number of hatchlings per cocoon increased only slightly, the production of hatchlings did not reach the initial level ($p > 0.05$). Reproductive output declined, however, in June-July. Also sterility rose considerably at that time; 15-20 % as compared to 0-10 % earlier.

3.8. CAN FAVOURABLE FOOD AND TEMPERATURE CONDITIONS CHANGE THE LONGEVITY OF *D. LACTEUM* AND MAKE IT ITEROPAROUS?

Given the standard ration of one *A. aquaticus* per tricland and week and a temperature of 5°C, the weekly average cocoon output, calculated on a monthly basis, varied as shown in Fig. 3. *D. lacteum* appeared to be able to reproduce for two years, and some of the specimens survived for more than three years. During the second year the reproductive output was, however, low in general and the number of hatchlings per cocoon was mostly around 5 (range 1-17). As sterility was high (70-90 %) during the second year, the total hatchling output was very low.

3.9. DOES *D. LACTEUM* HAVE AN INTRINSIC SEASONAL REPRODUCTIVE PATTERN?

Despite the fact that the rearing of the 5°C-animals was performed in complete darkness, a natural periodicity of the reproduction was discernible ($p < 0.001$), although somewhat displaced in time relative to the natural pattern (Fig. 3).

4. DISCUSSION

4.1. EFFECTS OF TEMPERATURE

Essentially, the experiments showed that temperature can regulate the timing of the reproduction in *D. lacteum*. Increase in tempera-

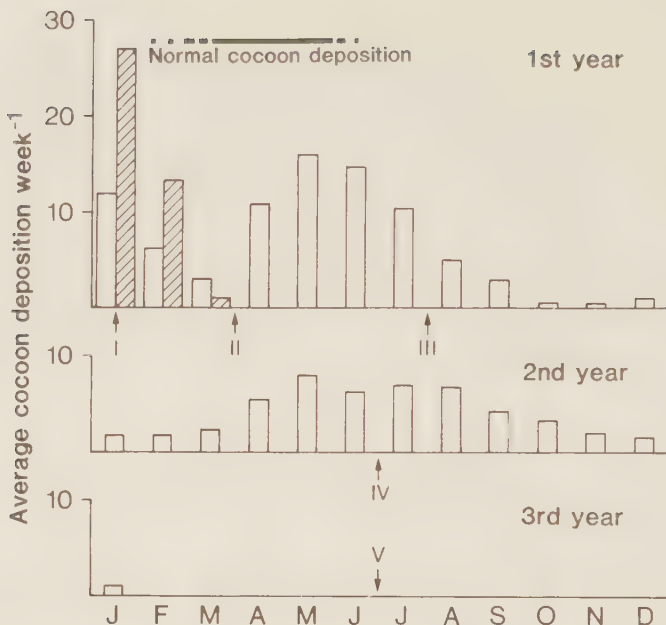


Fig. 3. Average weekly cocoon production, on a monthly basis, for *D. lacteum* at constant temperatures; 5°C (open bars) and 15°C (filled bars). Triclad numbers and feeding as in Fig. 2. I = Start of experiment; complete starvation to II. II = 15°C-animals lost. Feeding of 5°C-animals started (1 *A. aquaticus* per triclad and week). Run in total darkness from now on. III = Where Fig. 2 ends. 26 specimens still left. IV = 20 specimens left. V = End of experiment; 14 specimens left, of which 5 seemed to be in "good condition".

ture when early accelerated and when late retarded, respectively, cocoon and hatchling production (see 3.1). A very rapid temperature rise (Exp. 1E) promoted cocoon production, but the quality of the output - hatchlings per cocoon and the viability of the cocoons - declined pronouncedly. Temperatures around 10°C seemed most favourable (see 3.2), whereas temperatures below c. 2°C and over 20°C inhibited cocoon deposition, and impaired the adults (see 3.3). This concurs with the findings of Reynoldson et al. (1965).

The observations confirmed the predictions made in the Introduction, although a simulated cold and late spring seemed to present the most propitious temperature regime for reproductive suc-

cess when the entire period of reproduction is considered (see 3.5). In comparison with the output parameters for the natural temperature regime the differences were, however, not significant (Tab. 1, Exps A-C). One cautionary point should be made here. The constant food ration might be metabolically unsufficient at temperatures of 15-20°C. On the other hand, also in the field the cocoon output was highest at about 10°C and ended in June (Herrmann 1979, 1982a), although densities of A. aquaticus increased considerably in late spring (Friberg unpubl.).

In the field a long and delayed spring (see Fig. 1B) is nevertheless mostly followed by a "normal" summer. An unnaturally high proportion of newly hatched triclads would then be exposed to long periods of temperatures above 20°C (Herrmann 1979), to which hatchlings are vulnerable (Reynoldson et al. 1965). Moreover, a spring as in Fig. 1B would cause much longer incubation periods for the cocoons. These would then be exposed to probably higher risks of predation and infection, the latter indicated by Fig. 1).

An early or rapid spring, on the other hand, would cause a hatchling peak in the beginning of May, deduced from Fig. 1C and Herrmann (1982a). At that time the temperature will rapidly approach critical levels, not only for the hatchlings, but also for the remaining cocoons, as the sterility of these tends to increase with rising temperature (Herrmann 1982a, see also Pattee et al. 1973). Therefore, the results suggest that deviations from "normal" temperature conditions can be harmful to D. lacteum. By proper timing of the reproductive cycle in relation to and by means of the ambient temperature D. lacteum ensures that its vulnerable juvenile stages occur at an appropriate time of the year. The reproductive output of starving triclads also differed when exposed to different temperatures (Fig. 2). During the first month significantly more cocoons were produced by animals that were kept at 15°C as compared with those kept at 5°C (see 3.6). The number of hatchlings per cocoon was, however, significantly higher in the 5°C regime and these cocoons also showed a tendency of higher viability (Fig. 2). A higher temperature obviously favours cocoon production, but each cocoon yields fewer hatchlings. At times of food scarcity, triclads are able to breed by resorption, even if to a reduced extent (Woollhead and Calow 1979). This resorption, like all metabolic processes, will affect the adults more at a higher temperature (see Fig. 2). Consequently, some weeks' starvation is more serious for the adults at a higher temperature.

Calow and Woolhead (1977) stated that mortality must be viewed as the joint effect of starvation and reproduction. I agree that at least life expectancy could be ruled by these, which would reinforce the need for D. lacteum to terminate its reproduction before the temperature becomes too high, as stated above.

Thus, within limits, D. lacteum produces offspring under conditions of food scarcity. In March cocoon production ceased more drastically for the triclads reared at 15°C than those reared at 5°C (Fig. 2). At this time animals in both groups were considerably shrunken and in bad condition, resembling animals obtained in June in Lake Bysjön (Herrmann 1979). The ability of D. lacteum to reproduce after some time of food shortage also depends on temperature. In fact, Woolhead and Calow (1979) found that the semelparous and annual D. lacteum increased its reproductive effort as food supply decreased, as opposed to the iteroparous and perennial Polycelis tenuis Ijima, which invested a rather constant effort in reproduction. The former was referred to as "recklessness" and the latter "restraint".

Cocoon deposition of D. lacteum in Sweden normally takes place from mid March to the end of May (Herrmann 1979, 1982a). Although the potential stimuli were kept constant in the present long-term experiment, D. lacteum showed a tendency to increase cocoon output in April and to decrease it in July-September (Fig. 3). There seems to exist an intrinsic biological clock for initiation and termination of the reproduction.

The reproductive events and their outcome are thus largely dependent upon the temperature, but of course also the food availability (see Herrmann 1982b). A third possibility is that the age of the adults per se influences the egg production. This is compatible with the hypothesis that the termination of the reproduction is "regulated endogenously" (Herrmann 1979; Calow pers. comm.).

The number of cocoons deposited weekly (c/w) and number of hatchlings per cocoon (h/c) can be used for a tentative comparison of the role of temperature and age in regulating the reproductive output. Data on c/w and h/c from Exps A-C (Fig. 1) were thus compared: 1/. The first week in April, when the three different temperature trends had operated for four weeks. A difference in c/w or h/c should indicate regulation by temperature, whereas relative similarity should indicate regulation by age. 2/. The first week in May, when the temperature differences had become

more pronounced. Indications as above. 3/. The week in each experiment when the average temperature reached 10°C , regarded as the most optimal temperature, see above. In this case a difference in c/w or h/c should indicate regulation by age, whereas relative similarity should indicate regulation by temperature. The observed values are presented in Tab. 2.

TABLE 2

Comparisons of average weekly cocoon production (c/w) and average number of hatchlings per cocoon (h/c) for different occasions on the basis of data taken from Exps A-C in Fig.1. Significances were tested by one-way ANOVA.

NS = Non-significant difference. A = Regulation by age proposed,
T = Regulation by temperature proposed. I, II = weeks number 1
and 2, respectively, for a certain month.

Analysis No.	Parameter/ Occasion	Experiment No			Signifi- cance	Interpreted as A or T
		1A	1B	1C		
1	c/w in April I	1.53 (6 ^o)	1.00 (3 ^o)	1.87 (10 ^o)	p<0.05	T (?)
2	c/w in May I	1.73 (10 ^o)	1.07 (6 ^o)	2.00 (19 ^o)	p<0.001	T
3	c/w at +10 ^o C	1.73 (May I)	1.66 (June II)	1.86 (April I)	NS	T
4	h/c in April I	17.6	18.1	15.8	NS	A
5	h/c in May I	11.8	13.9	9.7	p<0.001	T
6	h/c at +10 ^o C	11.7	7.6	15.8	p<0.001	A

According to Tab. 2, temperature seems to be more important in regulating the cocoon output, whereas age seems to be more important for the cocoon content. The age possibility is further supported by Fig. 1B, where c/w and h/c decreased at the correct time, even if temperature had just passed 10°C . However, most probably both factors as well as food and others govern the reproduction in different aspects.

4.2. WHY IS D. LACTEUM SEMELPAROUS?

Obviously, D. lacteum can reproduce during two consecutive years. About 20 % of the specimens survived for even three years in "good condition" (Fig. 3), but then reproduction had ceased. The pattern conforms with a suggestion by Calow (1977) that "prevention of reproduction significantly increases the longevity of semelparous females", since in my experiment the triclads, because of atypical temperature conditions, were prevented from using all their potential reproductive capacity. In Lake Bysjön D. lacteum very rarely lives for more than one year (Herrmann 1979), whereas in Britain up to perhaps 40 % can live for two years (Young and Reynolds 1966). In both areas, the natural mode of reproduction is semelparity, but the British population shows a tendency of iteroparity, by living two years.

However, since D. lacteum is able to reproduce during two years, and survive a third year of life under laboratory conditions, it might be asked why iteroparous populations of D. lacteum have never been observed, at least not in northern Europe. Interestingly, histological studies of the reproductive system of D. lacteum from a population from northern France implies a case of iteroparity (Stéphan-Dubois and Gusse 1974).

Calow et al. (1981), mainly comparing with P. tenuis, suggested that as D. lacteum has a high energy conversion efficiency and is regarded to be mainly a passive hunter, it can invest more energy in reproduction, resulting in more and larger offspring, which also grow and survive better at food shortage. This would benefit the parent to invest more energy in offspring, even if detrimental for itself. This recklessness increases the adult mortality and should cause the semelparity, whereas P. tenuis cannot afford this strategy.

Earlier I suggested that the D. lacteum population in Lake Bysjön showed more characteristic of r-selection, while British populations were more towards K-selection, labelled from aspects on reproductive strategies (Herrmann 1979). Born in mind the relativity of these concepts, the view seems legitimate as semelparity should characterize r-strategists and iteroparity K-strategists (Pianka 1974), underlined by the statement of Calow (1978) that one often finds an "inverse relationship between reproductive output and repeated breeding". The individual reproductive output of D. lacteum in Lake Bysjön is, because of food and temperature con-

ditions, high compared with corresponding values from Britain (Herrmann 1982a). According to the last sentence of the former paragraph, it then seems, because of this "relative recklessness" of a Swedish average specimen, as if the environmental conditions should depress any tendency of selection for iteroparity. The energetic cost for one adult to survive the winter is probably too high and thus no potential gain would be expected from an iteroparous strategy. Hence there should be a premium on a high progeny production and semelparity.

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CONTENTS

Preface	3 - 4
List of papers	5
Summary of results	6 - 14
Factors affecting the occurrence of <u>Dendrocoelum lacteum</u> (Turbellaria) in a South Swedish lake	15 - 26
Population dynamics of <u>Dendrocoelum lacteum</u> (O.F. Müller) (Turbellaria, Tricladida) in a South Swedish lake	27 - 55
Reproductive phenology in <u>Dendrocoelum lacteum</u> (Turbellaria)	57 - 70
Prey choice and its impact on the reproductive output in <u>Dendrocoelum lacteum</u> (Turbellaria)	71 - 87
Temperature-dependence of reproduction in <u>Dendrocoelum lacteum</u> (Turbellaria) - an experimental approach	89 - 104